Gondwana Research 119 (2023) 341–383

Contents lists available at ScienceDirect

Gondwana Research

journal homepage: www.elsevier.com/locate/gr

GR Focus Review

A review of the Jurassic and Cretaceous Gondwanan pterosaur record

Adele H. Pentland [a,b,*], Stephen F. Poropat [b,c]

[a] School of Science, Computing and Engineering Technologies, Swinburne University of Technology, John St, Hawthorn, Victoria 3122, Australia
[b] Australian Age of Dinosaurs Museum of Natural History, The Jump-Up, Winton, QLD 4735, Australia
[c] Western Australian Organic & Isotope Geochemistry Centre, Curtin University, Kent St, Bentley, Western Australia 6102, Australia

ARTICLE INFO

Article history:
Received 22 May 2022
Revised 2 March 2023
Accepted 2 March 2023
Available online 21 March 2023
Handling editor: Ian David Somerville

Keywords:
Araripe Basin
Gondwana
Pterosauria
Palaeobiogeography
Santana group

ABSTRACT

The Gondwanan pterosaur record is scarce when compared with that of Laurasia and is reviewed here. The majority of Gondwanan pterosaur remains are derived from South America; however, the relative richness of the South American record compared with other Gondwanan continents is largely a result of the 'Lagerstätten' effect. Nevertheless, the South American pterosaur assemblage represents the most speciose and diverse known from Gondwana, with several lineages represented, including the Raeticodactylidae, Rhamphorhynchoidea, Darwinoptera, Ctenochasmatidae, Gnathosaurinae, Nyctosauridae, Ornithocheiridae, Tapejaridae, Thalassodromidae, Dsungaripteridae, Chaoyangopteridae and Azhdarchidae. Gondwanan pterosauromorphs are known only from South America. From Africa rhamphorhynchids, archaeopterodactyloids, pteranodontians, nyctosaurids, ornithocheirids, tapejarids, dsungaripteroids, chaoyangopterids, and azhdarchids have been reported. The Arabian Peninsula has produced nyctosaurids, an istiodactyliform, ornithocheirids and azhdarchids. Non-pterodactyloid pterosaurs have been reported from India. A possible azhdarchid has been reported from Madagascar and rhamphorhynchids are known from isolated teeth. The Antarctic pterosaur assemblage also comprises isolated remains of indeterminate pterodactyloids, and a possible indeterminate rhamphorhynchoid. The pterosaur record from East Gondwana comprises ornithocheirids, azhdarchids and a possible ctenochasmatoid from Australia, as well as azhdarchids from New Zealand. Although our understanding of Gondwanan pterosaurs has greatly improved within the last three decades, the discovery and description of more specimens, particularly from Antarctica and East Gondwana, will enhance our understanding of pterosaurian biodiversity and palaeobiogeography.
© 2023 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.

Contents

1. Introduction . . . 343
2. Methods . . . 344
3. South America . . . 344
 3.1. Triassic pterosaurs of South America . . . 344
  3.1.1. Quebrada del Barro Formation, Argentina . . . 344
  3.1.2. Caturrita Formation, Brazil . . . 345
 3.2. Jurassic pterosaurs of South America . . . 345
  3.2.1. Cañadón Asfalto Formation of Chubut, Argentina . . . 345
  3.2.2. Lotena Formation¸ Argentina . . . 345
  3.2.3. Cerro Campamento Formation, Chile . . . 345
  3.2.4. Vaca Muerta Formation, Patagonia . . . 345
 3.3. Cretaceous pterosaurs of South America . . . 346
  3.3.1. Recôncavo Basin, Brazil . . . 346
  3.3.2. Quebrada Monardes Formation, Chile . . . 346
  3.3.3. Rosablanca Formation, Colombia . . . 347

* Corresponding author at: School of Science, Computing and Engineering Technologies, Swinburne University of Technology, John St, Hawthorn, Victoria 3122, Australia.
E-mail address: apentland@swin.edu.au (A.H. Pentland).

https://doi.org/10.1016/j.gr.2023.03.005
1342-937X/© 2023 International Association for Gondwana Research. Published by Elsevier B.V. All rights reserved.

3.3.4. Tacuarembó Formation, Uruguay . . . 347
3.3.5. Totoralillo Formation, Chile . . . 347
3.3.6. La Amarga Formation, Argentina . . . 347
3.3.7. Río Belgrano Formation, Argentina . . . 347
3.3.8. La Cruz Formation, Argentina . . . 348
3.3.9. Apón Formation, Venezuela . . . 348
3.3.10. Araripe Basin, Brazil . . . 348
3.3.11. The Santana Group, Brazil . . . 351
3.3.12. Lohan Cura Formation, Argentina . . . 357
3.3.13. Goio-Erê Formation, Brazil . . . 358
3.3.14. Lagarcito Formation, Argentina . . . 358
3.3.15. Chulec Formation, Peru . . . 359
3.3.16. Exu Formation, Brazil . . . 359
3.3.17. Alcântara Formation, Brazil . . . 359
3.3.18. Candeleros Formation, Argentina . . . 359
3.3.19. Bajo Barreal Formation, Argentina . . . 359
3.3.20. Portezuelo Formation, Argentina . . . 359
3.3.21. Plottier Formation, Argentina . . . 359
3.3.22. Bajo de la Carpa Formation, Argentina . . . 359
3.3.23. Anacleto Formation, Argentina . . . 360
3.3.24. Allen Formation, Argentina . . . 360
3.3.25. Uncertain stratum, Brazil . . . 360
4. Africa . . . 360
4.1. Jurassic pterosaurs of Africa . . . 360
4.1.1. Upper Elliot Formation, South Africa . . . 360
4.1.2. Clarens Formation, South Africa . . . 360
4.1.3. Anoual Formation, Morocco . . . 360
4.1.4. Tendaguru Formation, Tanzania . . . 360
4.2. Cretaceous pterosaurs of Africa . . . 361
4.2.1. Upper Lualaba Series, Congo . . . 361
4.2.2. High atlas Mountains, Morocco . . . 361
4.2.3. Douiret Formation, Tunisia . . . 361
4.2.4. Elrhaz Formation, Niger . . . 361
4.2.5. Chenini Formation, Tunisia . . . 361
4.2.6. Aïn el Guettar Formation, Tunisia . . . 361
4.2.7. Gara Samani Formation, Algeria . . . 361
4.2.8. Kem Kem Group, Morocco . . . 361
4.2.9. Turkana Grits, Kenya . . . 363
4.2.10. Western high Atlas, Morocco . . . 364
4.2.11. Paki Formation, Senegal . . . 364
4.2.12. Logbadjeck Formation, Cameroon . . . 364
4.2.13. Mocuio Formation, Angola . . . 364
4.2.14. Oulad Abdoun Basin, Morocco . . . 364
4.2.15. Tagragra Formation, Morocco . . . 365
5. Arabian Peninsula . . . 365
5.1. Ein-Yabrud, Jerusalem . . . 365
5.2. Hâqel Lagerstätte, Lebanon . . . 365
5.3. Hjoûla Lagerstätte, Lebanon . . . 365
5.4. Mishash Formation, Israel . . . 365
5.5. Phosphate Deposits, Jordan . . . 366
5.6. Muwaqqar Chalk Formation, Jordan . . . 366
6. Madagascar . . . 366
6.1. Mahajanga *Basin,* Madagascar . . . 366
6.2. Morondava Basin, Madagascar . . . 366
7. Indo-Pakistan subcontinent . . . 366
7.1. Kota Formation, India . . . 366
7.2. Samana Suk Limestone, Pakistan . . . 367
7.3. Lameta Formation, India . . . 367
7.4. Vitakri Formation, Pakistan . . . 367
8. Australia . . . 367
8.1. Eumeralla Formation . . . 367
8.2. Toolebuc Formation . . . 367
8.3. Griman Creek Formation . . . 372
8.4. Mackunda Formation . . . 372
8.5. Winton Formation . . . 372
8.6. Molecap Greensand . . . 372
8.7. Miria Formation . . . 373
9. New Zealand . . . 373
9.1. Maungataniwha sandstone member, tahora formation . . . 373
10. Antarctica . . . 373
10.1. Hanson Formation, Antarctica . . . 373
10.2. Santa Marta Formation, Antarctica . . . 373

10.3. Snow Hill Island Formation, Antarctica . . . 373
11. Discussion . . . 374
12. Conclusion . . . 375
Declaration of Competing Interest . . . 375
Acknowledgements . . . 376
Appendix A. Supplementary data . . . 376
References . . . 376

1. Introduction

Pterosaur fossils have been discovered on every continent, including Antarctica (Barrett et al., 2008; Upchurch et al., 2015). Pterosaurs first appeared in the Norian (Late Triassic) and experienced rapid diversification during the Jurassic, before becoming extinct at the end of the Cretaceous (Dalla Vecchia, 2013; Padian, 1985; Unwin, 2005; Wellnhofer, 1991b; Witton, 2013). The earliest reports of pterosaur remains were made in Europe in the late 18th Century and early 19th Century (e.g., Collini, 1784; Cuvier, 1809; see Wellnhofer, 1991b) and Wellnhofer (2008) for an overview). The first reports of pterosaur remains outside of Europe were published in North America by Marsh (1872) and Cope (1871), with both workers describing fossils from the Upper Cretaceous Niobrara Chalk of Kansas. By contrast, the first Gondwanan pterosaur remains were not recognised until the 20th Century (Mawson and Smith Woodward, 1907).

The extremely fragile nature of pterosaur material is the principal reason for their relative scarcity in the fossil record (Kellner, 1994). Thus far, relatively few deposits are known worldwide from which partial skeletons have been found in abundance. These include the Upper Triassic Dolomia di Forni Formation of Italy (e.g. Dalla Vecchia, 2019), the Lower Jurassic Posidonia Shale Formation (Padian, 2008a, b), the Upper Jurassic Tiaojishan Formation (Lü et al., 2010a; Lü and Fucha, 2010; Lü et al., 2012), the Upper Jurassic Solnhofen deposits of Germany (e.g. Wellnhofer, 1970, 1991c), the Lower Cretaceous Crato and Romualdo lagerstätten of the Santana Group in Brazil (e.g. Martill and Frey, 1998; Wellnhofer and Kellner, 1991), the Lower Cretaceous Jiufotang and Yixian formations of China (e.g. Wang et al., 2005), and the Upper Cretaceous Niobrara Chalk in North America (e.g. Bennett, 2001). The Lower Cretaceous Lagarcito Formation of Argentina has also produced near-complete pterosaur specimens, juveniles and unhatched pterosaur eggs (Chiappe et al., 2004; Codorniú and Chiappe, 2004b; Codorniú et al., 2016b; Grellet-Tinner et al., 2014), thus enhancing our understanding of pterosaur ontogeny (Chinsamy et al., 2009). Despite the relative abundance of pterosaur material in some localities, such as the mid-Cretaceous Cambridge Greensand in the United Kingdom, the majority of localities yield only fragmentary and isolated pterosaur remains (Costa and Kellner, 2009; Kellner, 2003a,b; Unwin, 2001).

Although the Gondwanan pterosaur record was reviewed by Kellner (2001b), our understanding of these winged reptiles has changed considerably over the last twenty years with the discovery of additional material, particularly partial skeletons. As stated by Barrett et al. (2008), deposits in Australia, Antarctica, Africa and South America constitute only 12% of the world's pterosaur localities. Although many more pterosaurs have been reported since then, at present, we know comparatively little about the Gondwanan pterosaur record when compared with remains from Europe, Asia, and North America. Unfortunately, our understanding of Gondwanan pterosaur diversity has been distorted as the result of sampling biases, as well as pervasive historical and socioeconomic factors (Raja et al., 2021). At present, the majority of Gondwanan pterosaur localities are Cretaceous in age, with few specimens from the Jurassic (Martínez et al., 2015b). Italy notwithstanding (Kellner, 2015; Upchurch et al., 2015), little evidence of pterosaurs has been found in Triassic strata in Gondwana (Dalla Vecchia, 2013). Despite the fact that relatively few Gondwanan pterosaur localities are known by comparison with Europe, Asia and North America, these deposits have nevertheless provided valuable insights into several pterosaur clades. The aim of this review is to provide a comprehensive summary of the pterosaur body and trace fossils reported from Gondwana and comment on their taxonomic relationships.

Institutional abbreviations. AMNH, American Museum Natural History, New York, U.S.A.; AODF, Australian Age of Dinosaurs Natural History Museum Fossil, Winton, Queensland, Australia; AODL, Australian Age of Dinosaurs Natural History Museum Locality, Winton, Queensland, Australia; BHI, Black Hills Institute of Geological Research, Hill City, South Dakota, U.S.A.; BMNH, British Museum of Natural History, London, U.K.; BSP, Bayerische Staatsammlung für Paläontologie und historische Geologie, Munich, Germany; CAMSM, Sedgwick Museum, Cambridge, U.K.; CCMGE, Chernyshev's Central Museum of Geological Exploration, St. Petersburg, Russia; CD, Desirée Collection of Rainer Alexander von Blittersdorff, Rio de Janeiro, Brazil; CCSRL, Centro Studi e Ricerche Ligabue, Venice, Italy; CMN Canadian Museum of Nature, Ottawa, Canada (formerly NMC); CP, Centro Paleontológico (CENPALEO) of the Universidade do Contestado, Mafra, Santa Catarina, Brazil; CPCA, Centro de Pesquisas Paleontológicas da Chapada do Araripe, Crato, Brazil; CTES-PZ, Laboratorio de Paleozoología, Departamento de Biología, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, Argentina; DGEO-CTG-UFPE, Departamento de Geologia, Centro de Tecnologia e Geociências, Universidade Federal de Pernambuco, Recife, Brazil; DGM, Museum de Ciencia da Terra/Departmento Nacional Producao Mineral, Rio de Janeiro, Brazil; FC-DPV, Fossil Collections of Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay; FML Fundaci6n Miguel Lillo, Tucuman, Argentina; FSA, Faculté des Sciences, Université Ibn Zohr, Agadir, Morocco; FSAC, Faculté des Sciences Ain Chock, Université Hassan II, Casablanca, Morocco; GEA, Guelb el Ahmar, Morocco; GNS CD, GNS Science, Lower Hutt, New Zealand; GP, Coleção de Paleontologia Sistemática of the Geosciences Institute of Universidade de São Paulo, Brazil; GSI, Geological Survey of India, Kolkata, India; IMCF/IMNH, Iwaki City Coal and Fossil Museum, Iwaki, Japan; ISI, Indian Statistical Institute, Kolkata, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; China; JZMP, Jinzhou Paleontological Museum, Liaoning Province, China; KNM-WT, Kenya National Museum, West Turkana, Kenya; KPMNH DL, Kanagawa Prefectural Museum of Natural History, Japan; LGS, Laboratoire de Géomatique, Écologie et Environnement, Gara Samani, Algeria; LINHM, Long Island Natural History Museum, New York City, U.S.A.; LRF, Australian Opal Centre, Lightning Ridge, New South Wales, Australia; NMSG, Naturmuseum St. Gallen, St. Gallen, St. Gallen Canton, Switzerland; MACN, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina; MB.R., Collection of Fossil Reptilia, Museum für Naturkunde (MfN), Berlin, Germany; MBLUZ, Museo de Biologia, Universidad del Zulia, Maracaibo, Vene-

zuela; MCF-PVPH, Museo Carmen Funes-Paleontología de Vertebrados, Plaza Huincul, Neuquén Province, Argentina; MCT, Museu Ciencias da Terra, Setor de Paleontologia, Departmento Nacional da Producão Mineral, Rio de Janeiro, Brazil; MGUAN-PA, Museu de Geologia da Universidade Agostinho Neto, Luanda, Angola (PaleoAngola Collection); MHIN-UNSL-GEO-V, Museo de Historia Natural, Universidad Nacional de San Luis, San Luis, Argentina; MHNS, Museum of Natural History Sintra, Portugal; MIM, Mineral Museum of Beirut, Lebanon; MIC, Museo Interactivo de Ciencias, Universidad Nacional de San Luis, San Luis, Argentina; MMCh, Museo Municipal Ernesto Bachmann, Villa El Chocón, Neuquén, Argentina; MMP, Museo Municipal de Ciencias Naturales "Galileo Scaglia," Mar del Plata, Argentina; MN, Museum für Naturkunde, Berlin, Germany (formerly HMN, Humboldt Museum für Naturkunde); MNN, Musée National du Niger, Niamey, Republic of Niger; MOR, Museum of the Rockies, Bozeman, Montana, U.S.A.; MOZ, Museo de la Dirección Provincial de Minería, Zapala, Neuquén, Argentina; MPEF, Museo Paleontológico "Egidio Feruglio", Trelew, Chubut, Argentina; MPCN-PV, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina; MPSC, Museu de Paleontologia de Santana do Cariri, Santana do Cariri, Brazil; MSM, Museum of Geological Survey of Pakistan, Sariab Road, Quetta, Pakistan; MSNM, Museo Civico di Storia Naturale di Milano, Italy; MTM, Hungarian Natural History Museum, Budapest, Hungary; MUCPv Museo de Geologia y Paleontologia de la Universidad Nacional del Comahue, Paleontologia de Vertebrados, Neuquén Province, Argentina; MZ, Institut und Museum für Paläontologie der Universität Zürich, Zurich, Switzerland; OCP DEK, Office Chérifien des Phosphates, Service Géologique, Khouribga, Morocco; NHMUK, Natural History Museum, London, U.K.; NMV, National Museum of Victoria, Melbourne, Victoria, Australia; PVL, Fundacion Miguel Lillo, Universidad Nacional de Tucuman, San Miguel de Tucuman, Argentina; PVSJ, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; QM, Queensland Museum, Brisbane, Queensland, Australia; QM F, Queensland Museum Fossil; RGM, Nationaal Natuurhistorisch Museum (Naturalis), Leiden, The Netherlands; RH, Mémoire de la terre, Museum Tataouine, C207 Tatouine, Tunisia; SA, Laboratoire de paleontologie, Museum national d'histoire naturelle, Paris, France; SAM, South Australian Museum, Adelaide, South Australia, Australia; SAO/UOSG, Sammlung Urs Oberli, St. Gallen, St. Gallen Canton, Switzerland; SGO.PV Área Paleontología de Vertebrados, Museo Nacional de Historia Natural, Santiago, Chile; SMNK, Staatliches Museum für Naturkunde, Karlsruhe, Karlsruhe, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, U.S.A.; TsNIGRI, LU-N, Tsentral'nyy nauchno-issledovatel'skiy Geologorazvedochnyy Institut Tsvetnykh, Moscow, Russia; UCMP, University of California, Museum of Paleontology, Berkeley, U.S.A.; UCRC University of Chicago Research Collection, Chicago, U.S.A.; UFRGS. PV, Department of Geology, Universidade Federal de Rio Grande do Sul, Porto Alegre, Brazil; UNCUYO-LD, Universidad Nacional de Cuyo, Instituto de Ciencias Basicas, Laboratorio de Dinosaurios, Mendoza, Argentina; UJ/VF, University of Jordan, department of Geology, Amman, Jordan; UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Argentina; UOP, University of Portsmouth School of Earth and Environmental Sciences, U.K.; UR CP, Paleontological Collection Universidad del Rosario, Bogotá, Colombia; URC, Instituto de Geociências e Ciências Exatas da Universidade Estadual Paulista (UNESP), Rio Claro, State of São Paulo; UvA M, Geological Institute of the University of Amsterdam, Amsterdam, The Netherlands; WAM, Western Australian Museum, Perth, Western Australia, Australia; YPM, Yale Peabody Museum, New Haven, Connecticut, U.S.A; ZIN PH: Palaeoherpetological collection, Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia.

2. Methods

Following Bestwick et al. (2018a), Pterosauria is defined as *Preondactylus buffarinii*, *Quetzalcoatlus northropi*, their common ancestor and all of its descendants. Although there is a consensus regarding the taxonomic content of most major pterosaur clades, we note that the major pterosaurian phylogenetic analyses differ slightly (Andres et al., 2014; Kellner, 2003a,b; Lü et al., 2010b; Unwin, 2003). The taxonomic nomenclature used herein follows that of the most recent comprehensive phylogenetic analysis (Andres, 2021). We follow Ezcurra et al. (2020), such that the Pterosauromorpha includes the Pterosauria and Lagerpetidae. Following Nesbitt (2009) Lagerpetidae is defined as *Lagerpeton chanarensis*, *Dromomeron romeri* and *Dromomeron gregorii*, their common ancestor and all of its descendants. Pterodactyloidea is defined as the most inclusive clade with a metacarpus 80% or more than the length of the humerus, synapomorphic with *Pterodactylus antiquus* Sömmering, 1812 (*sensu* Padian, 2004). The other major clades discussed in the present work include the Raeticodactylidae, Rhamphorhynchoidea, Darwinoptera, Archaeopterodactyloidea, Ctenochasmatidae, Gnathosaurinae, Ornithocheiroidea, Pteranodontia, Nyctosauridae, Istiodactyliformes, Ornithocheiridae, Azhdarchoidea, Tapejaridae, Thalassodromidae, Dsungaripteroidea, Chaoyangopteridae, and Azhdarchidae.

3. South America

The South America pterosaur record is undoubtedly the most diverse and well-researched Gondwanan pterosaur assemblage, with members of the Raeticodactylidae, Ctenochasmatidae, Gnathosaurinae, Nyctosauridae, Ornithocheiridae, Tapejaridae, Thalassodromidae, Dsungaripteridae and Azhdarchidae represented (Martill et al., 2000; Martill et al., 2006; Martínez et al., 2022; Perea et al., 2018; Soto et al., 2021). The majority of specimens are derived from Cretaceous sedimentary rocks deposited in the Araripe Basin of Brazil, which has yielded numerous partial skeletons (Elgin and Frey, 2012) and specimens preserving soft-tissues (Campos et al., 1984; Campos and Kellner, 1997; Campos et al., 2017; Frey and Martill, 1994; Frey et al., 2003b; Frey et al., 2003c; Kellner, 2004; Martill and Unwin, 1989). The South American pterosaur assemblage has also been fundamental to augmenting our understanding of pterodactyloid head crest morphology (Campos and Kellner, 1997; Wellnhofer and Kellner, 1991) and wing membrane extent (Campos et al., 1984; Frey and Martill, 1994; Frey et al., 2003c).

3.1. Triassic pterosaurs of South America

3.1.1. Quebrada del Barro Formation, Argentina

The geologically oldest South American pterosaur remains are from the Late Triassic (Norian-Rhaetian) Quebrada del Barro Formation of Argentina (Martínez et al., 2015b). They comprise a partial rostrum with premaxillary crest (PVSJ 914) and the proximal end of a possible right ulna (PVSJ 913). More recently, both specimens were described in further detail by Martínez et al. (2022), along with a partial jaw recovered from a different locality (PVSJ 1080). PVSJ 913 is three-dimensionally preserved and preserves the diaphysis and distal articular surface (Martínez et al., 2015b). Histological analysis of PVSJ 913 indicates that the orientation of the cortical bone differs from that typically observed in pterosaurs, and more closely resembles 'crossed parallel' bone (Martínez et al., 2022). PVSJ 914 was designated the holotype specimen of a new taxon *Yelaphomte praderioi*, and differs from other taxa in that the premaxillary crest bears a series of thin, radial grooves on the lateral surface (Martínez et al., 2022). A second taxon was

established, *Pachagnathus benitoi* (PVSJ 1080) based on a partial mandibular symphysis preserving a partial *in situ* tooth (Martínez et al., 2022). *Yelaphomte* differs from *Pachagnathus*, in that the latter possesses cheek alveoli, as well as other aspects of its dentition (Martínez et al., 2022). *Yelaphomte* and *Pachagnathus* were resolved in a polytomy within the Raeticodactylidae (Martínez et al., 2022).

3.1.2. Caturrita Formation, Brazil

Faxinalipterus minima (UFRGS PV0927T; Bonaparte et al., 2010) was established on the basis of a partial postcranial skeleton derived from the lower Norian (see Kellner et al., 2022 and references therein) Caturrita Formation, northeast of Faxinal do Soturno, Rio Grande do Sul, Brazil. UFRGS PV0927T comprises a partial left coracoid, the proximal end of a left humerus, incomplete left radius and ulna, putative medial and distal fragments of the right humerus and near-complete left femur, tibia and fibula associated with a putative metatarsal and indeterminate fragments (Bonaparte et al., 2010). Assignment of UFRGS PV0927T to the Pterosauria was primarily based on the saddle-shaped morphology of the proximal articular head (Bonaparte et al., 2010), a common character in pterosaur humeri (Wellnhofer, 1978), as well as the morphology of the coracoid. Bonaparte et al. (2010) also noted hollow appendicular bones bearing thin diaphyseal walls, another characteristic of the Pterosauria. A partial left maxilla (UFRGS PV0769T) collected from the same locality and preserved in a separate sandstone block was tentatively referred to '*Faxinalipterus*', on the basis of its small size and 'characters of the teeth' (Bonaparte et al., 2010). The maxilla preserves three teeth, two of which are complete and long, thin and posteriorly curved (Bonaparte et al., 2010). At the time of publication, approximately 18 alveoli were observed (Bonaparte et al., 2010). More recently, the pterosaurian affinities of '*Faxinalipterus*' have been questioned by Dalla Vecchia, 2013; Soares et al., 2013. Soares et al., 2013 noted after further preparation that the humeral head is not saddle-shaped and the humerus lacks the distinct deltopectoral crest. Similarly, after firsthand observation of UFRGS PV0927T, Dalla Vecchia (2013) noted that the humerus was unlike that of any Triassic pterosaur material. More recently, additional preparation of the holotype specimen, combined with phylogenetic analysis, indicates that *Faxinalipterus* is a member of the Lagerpetidae and is not a pterosaur (Kellner et al., 2022). Moreover, the maxilla previously referred to *Faxinalipterus* (UFRGS-PV-0769-T) was designated the holotype of a new pterosauromorph taxon (*sensu* Ezcurra et al., 2020), *Maehary bonapartei*. The position of *Maehary* as the earliest member of the Pterosauromorpha is supported by phylogenetic analysis, conducted by Kellner et al. (2022).

3.2. Jurassic pterosaurs of South America

The South American Jurassic pterosaur record is sparse, with three taxa recognised, 1) *Allkaruen koi* (Codorniú et al., 2010; Codorniú et al., 2011; Codorniú et al., 2016a), 2) *Herbstosaurus pigmaeus* (Casamiquela, 1975; Unwin, 1996), and 3) *Wenupteryx uzi* (Codorniú and Gasparini, 2012).

3.2.1. Cañadón Asfalto Formation of Chubut, Argentina

Pterosaur remains from Middle Jurassic (Toarcian–Bathonian) Cañadón Asfalto Formation of Chubut, Argentina were first reported from near the village of Cerro Condor at the start of the 21st Century, and were described as disarticulated, but well-preserved in limestone (Rauhut and Puerta, 2001). Further remains from the same locality were reported by Unwin et al. (2004), who noted hundreds of disarticulated pterosaur bones (including several mandibles, a braincase, pectoral girdle and forelimb elements). These elements were tentatively referred to a rhamphorhynchoid with a wingspan of 1.5–2 m (Unwin et al., 2004). Unwin et al. (2004) noted that the morphology of the humerus and shoulder girdle are comparable with those known from *Scaphognathus*.

Allkaruen koi was established on the basis of a braincase (MPEF-PV 3613), mandible (MPEF-PV 3609), and a cervical vertebra (MPEF-PV 3615) from the Cañadón Asfalto Formation of Chubut, Argentina (Codorniú et al., 2016a). A second cervical vertebra (MPEF-PV 3616) was also referred to this taxon (Codorniú et al., 2016a). In contrast to the endocasts of *Rhamphorhynchus* and *Anhanguera*, that of *Allkaruen* demonstrates both plesiomorphic and derived characters of the inner ear and neuroanatomy, with four characters demonstrating an intermediate condition (Codorniú et al., 2016a). In one phylogenetic analysis, Wang et al. (2017) suggested that *Allkaruen* and *Douzhanopterus* were effectively indistinguishable based on the presently available fossil material. However, given that *Douzhanopterus* is separated from *Allkaruen* both spatially (China vs. Argentina) and temporally (early Late Jurassic vs. Middle Jurassic), it seems unlikely that these taxa are conspecific. More recently, Martin-Silverstone et al. (2022) resolved *Allkaruen koi* within the Darwinoptera.

3.2.2. Lotena Formation¸ Argentina

The first pterosaur taxon recognised from the Jurassic of South America, *Herbstosaurus pigmaeus* (CTES-PZ 1709), was established on the basis of a sacrum, incomplete prepubis, fragments of the right ilium, impression and sedimentary infill of the right femur, and impression of the left femur (Casamiquela, 1975). The specimen was found in a sandstone nodule from the upper Callovian Lotena Formation (Zanettini et al., 2010) of Neuquén Province, Argentina and was originally described as a coelurosaur with affinities close to *Compsognathus* (Casamiquela, 1975). It was not until 1978 that a pterosaurian position was posited by Ostrom (1978), who expressed doubts over its dinosaurian affinities, in particular based on the morphology of the femur and ilium. Bonaparte (1978) then assigned CTES-PZ 1709 to the Pterosauria based on the general morphology of the pelvis, as well as the proximal end of the femur, suggesting affinities with the Pterodactyloidea. Wellnhofer (1991b) noted the morphology of the pelvis and femur of *Herbstosaurus* were similar to those of the Rhamphorhynchoidea, but Unwin (1996) suggested the femur is more similar to the dsungaripteroids (*Germanodactylus* and *Dsungaripterus*). The general disagreement among pterosaur workers on the placement of *Herbstosaurus* within the Pterosauria is a consequence of the incompleteness of the holotype specimen.

3.2.3. Cerro Campamento Formation, Chile

A partial pterosaur skeleton, represented by the left humerus, a partial probable dorsal vertebra, and the diaphysis of a wing phalanx (MUHNCAL.20165) was recently described by Alarcón-Muñoz et al. (2021) from the Oxfordian Cerro Campamento Formation of Chile. The material is referrable to the Rhamphorhynchoidea, based on the hatchet-shaped deltopectoral crest of the humerus and presence of asymmetric crests either side of a groove on the posterior surface of the wing phalanx (Alarcón-Muñoz et al., 2021).

3.2.4. Vaca Muerta Formation, Patagonia

The most complete Jurassic pterosaur reported from the Southern Hemisphere, *Wenupteryx uzi* (MOZ-PV 3625), is interpreted as a pterodactyloid with an estimated wingspan of 1.1 m (Codorniú et al., 2006; Codorniú and Gasparini, 2012). The holotype specimen comprises a nearly complete postcranial skeleton recovered from the Tithonian (Leanza and Zeiss, 1992; Scasso and Concheyro, 1999) Vaca Muerta Formation of the Neuquén Basin, northwest Patagonia (Codorniú et al., 2006). The holotype is interpreted as a subadult individual on the basis of several unfused pelvic elements

(Codorniú et al., 2006; Codorniú and Gasparini, 2012). Additional elements pertaining to other individuals from the Tithonian Vaca Muerta Formation include the impression of a large tibiotarsus (MOZ-PV 094; Codorniú and Garrido, 2013; Codorniú and Gasparini, 2012) and a specimen originally described as a partial right tibia (MOZ-PV 2280; Gasparini et al., 1987). Based on comparisons with *Wenupteryx uzi*, MOZ-PV 094 is approximately two and a half times larger and represents a medium-sized pterodactyloid — potentially the largest Late Jurassic pterosaur from Gondwana (Codorniú and Gasparini, 2012). MOZ-PV 2280 was reinterpreted by Codorniú and Gasparini, 2012 as an incomplete ulna, from an individual larger than MOZ-PV 3625, which they referred to *Wenupteryx*.

3.3. Cretaceous pterosaurs of South America

Our understanding of Cretaceous pterosaurs from Gondwana has largely been influenced by the exceptional quality and sheer volume of material described from South America. Although this is undoubtedly because of the 'Lagerstätten' effect, with the majority of specimens from the Araripe Basin, the South American pterosaur assemblage has not only enhanced our understanding of their Gondwanan biodiversity, but life history. The Loma del *Pterodaustro* site has shed much-needed light on the ontogeny and neonatal development of *Pterodaustro* (Chiappe et al., 1998b; Chinsamy et al., 2008; Codorniú and Chiappe, 2004a; Codorniú et al., 2017). Similarly, the discovery of hundreds of pterosaur bones interpreted as the remains of a colony or colonies offers a tantalising but brief glimpse into pterosaur social behaviour (Bell and Padian, 1995). Although limited information can be gleaned from isolated pterosaur occurrences, each element adds to our knowledge of these winged reptiles and the environments they inhabited.

3.3.1. Recôncavo Basin, Brazil

The first report of pterosaur material from South America, and indeed, Gondwana, was an isolated tooth collected from the Lower Cretaceous (Berriasian–Hauterivian; Britto et al., 2022) Recôncavo Basin (State of Bahia, northeastern Brazil), which was mentioned but not described by Mawson and Smith Woodward (1907). Following Rodrigues and Kellner (2010), it is likely that the tooth mentioned by Mawson and Smith Woodward (1907) is NHMUK PV R8662 and is regarded as an indeterminate ornithocheirid, based on comparisons with other members of that clade. Rodrigues and Kellner (2010) also figured and described a second ornithocheirid tooth (NHMUK PV R3221) collected by Mawson; however, the specimen was previously regarded as a crocodilian until it was later identified by Dr Lorna Steel. The two teeth are similar in size, with NHMUK PV R8662 preserved in surrounding matrix and possessing longitudinal striations, whereas NHMUK PV R3221 is not as well-preserved, with no indication of striations on the worn external surface.

3.3.2. Quebrada Monardes Formation, Chile

Casamiquela et al., 1980 reported a fragmented mandibular symphysis, a partial left humerus and other postcranial elements from the Quebrada Monardes Formation of northern Chile (preserved in various rock fragments registered '250973' at the Antofagasta Regional Office of the Chilean Institute of Geological Research). The Quebrada Monardes Formation remains poorly constrained due to a lack of index fossils, but conformably overlies the Upper Jurassic marine sediments of the Lagunillas Formation, and is suggested to be upper Tithonian–lower Berriasian in age (Martínez et al., 2015a). These remains were assigned to the genus *Pterodaustro* based on the morphology of the humerus and mandible, despite the Quebrada Monardes specimen having a much lower tooth count than *Pterodaustro*. Martill et al. (2000) later interpreted the specimen as a dsungaripterid, because of alveolar protuberances and a sagittal crest bearing subparallel striations, and designated it as a new taxon, *Domeykodactylus ceciliae*. The presence of subparallel striations located on the cranial crest has been suggested as the insertion point for the soft-tissues of the premaxillary crest (Martill et al., 2000). The *Domeykodactylus ceciliae* type specimen demonstrates apomorphies of the Dsungaripteroidea, including an edentulous anterior tip of the mandibular symphysis and tooth size increasing posteriorly (Martill et al., 2000). The presence of expanded alveoli supports referral to the less inclusive Dsungaripteridae (Martill et al., 2000). The referral of *Domeykodactylus ceciliae* to the Dsungaripteridae has since been supported by a phylogenetic analysis by Andres et al. (2014).

In contrast to the isolated remains reported from other localities across the Quebrada Monardes Formation, thousands of isolated pterosaur bones have been reported from a 2 m thick sandstone and conglomerate bed in the Atacama Region of Chile (Bell and Padian, 1995). Given that fine-grained sandstone was observed above and below the fossil layer, combined with the occurrence of mudstone and calcrete rip-up clasts in the sandstone and conglomerate bed, it seems likely this material was deposited during a flood event (Bell and Padian, 1995). This dense accumulation of bones possibly deposited during a single event has been interpreted as the remains of a colony or colonies (Bell and Padian, 1995). Aside from the material demonstrating very thin cortical bone, the material has been regarded as pterosaurian based on the presence of cervical vertebrae with anteroposteriorly long centra and dorsoventrally short neural spines (Bell and Padian, 1995). Owing to the fragmentary and isolated nature of the remains, these were regarded as indeterminate pterodactyloids, on the basis that non-pterodactyloids are not known from the Cretaceous (Bell and Padian, 1995).

Two cervical vertebrae from Cerro La Isla (both originally registered as SGO.PV.350) have also been reported from the Quebrada Monardes Formation and interpreted as an indeterminate member of the Ctenochasmatidae (Rubilar et al., 2002). More recently, Alarcón-Muñoz et al. (2020) described these cervical vertebrae but noted that because of a lack of field data, it cannot be determined with certainty whether the two specimens were found in association and thus cannot be ascribed to the same individual. As such, one of these vertebra retained the original specimen number, SGO.PV.350, and the other was assigned a new specimen number, SGO.PV.351 (Alarcón-Muñoz et al., 2020). Referral to the Ctenochasmatidae is maintained based on the presence of low neural spines, and laterally positioned oval pneumatic foramina on SGO.PV.351, with both are regarded as members of the same taxon (Alarcón-Muñoz et al., 2020). The better-preserved vertebra (SGO.PV.350) is elongate such that the ratio between the centrum length (measured along the line of the hypapophysis) and its minimum width is 4.5 (Alarcón-Muñoz et al., 2020). Unfortunately, this observation is provisional, because of incomplete preservation of the left prezygapophysis (Alarcón-Muñoz et al., 2020). While the general morphology of SGO.PV.351 compares favourably with SGO.PV.350, the former is poorly preserved (Alarcón-Muñoz et al., 2020). SGO.PV.351 differs in that it is slightly more elongate, with the ratio between centrum length and minimum width equal to 5.8 (Alarcón-Muñoz et al., 2020). As noted by Alarcón-Muñoz et al. (2020), based on these ratios, SGO.PV.350 and SGO.PV.351 are less elongate than the mid cervical vertebrae of *Moganopterus* and *Elanodactylus*, but longer than those of *Gegepterus* and *Beipiaopterus* (Alarcón-Muñoz et al., 2020). However, as there is no standardised method for calculating the ratio of cervical vertebrae length and minimum width, comparison between ratios of different taxa must therefore be regarded provisional (Alarcón-Muñoz

et al., 2020). SGO.PV.351 is referred to the Ctenochasmatidae based on the presence of lateral pneumatic foramina; these features were not observed in SGO.PV.350, possibly because of compaction-induced fractures (Alarcón-Muñoz et al., 2020).

Additional ctenochasmatids from the Quebrada Monardes Formation include three partial symphysial jaws (SMNK-PAL 4012–4014) and the proximal end of a first wing phalanx (SMNK-PAL 4015) from the Cerro La Isla mesa (Martill et al., 2006). The extensor tendon process is fused to the first wing phalanx; however, a faint suture between the two is still visible, suggesting the individual was either an adult or near adult (Martill et al., 2006). All four specimens are incomplete and figured surrounded by matrix, with the three partial jaws visible in occlusal view; SMNK-PAL 4012 comprising the anterior end of the jaw (Martill et al., 2006). Although the precise position of SMNK-PAL 4014 cannot be determined with certainty, SMNK-PAL 4013 preserves the fragmentary remains of the left and right rami (Martill et al., 2006). The partial jaws are referred to the Ctenochasmatoidea, on the basis of their dentition comparable to *Ctenochasma* and *Gnathosaurus* from Upper Jurassic deposits in Europe (Martill et al., 2006). The spatulate rostrum of SMNK-PAL 4012 suggests affinities with *Gnathosaurus*; however, the tooth count in the three specimens is more similar to the Late Jurassic *Ctenochasma* (Martill et al., 2006). The unique dentition of SMNK-PAL 4012 prevents assignment to any known South American ctenochasmatid genera and suggests ctenochasmatids might have dispersed from Eurasia to Gondwana via South America (Martill et al., 2006).

As well as providing full descriptions for SGO.PV.350 and SGO.PV.351, Alarcón-Muñoz et al. (2020) described new material from the Cerro La Isla (Atacama Region, Northern Chile), collected during the same expedition. The new material figured and described includes a partial rostrum (SGO.PV.364) and fragmentary mandibles preserving alveoli and the eroded remnants of teeth (SGO.PV.362, SGO.PV.377 and SGO.PV.378). SGO.PV.364 was interpreted as the anterior end of a rostrum, based on the orientation of the alveoli and partial teeth therein. All four partial cranial elements were referred to the Ctenochasmatidae, based on the number of teeth relative to the preserved length of the jaw (Alarcón-Muñoz et al., 2020; Alarcón-Muñoz et al., 2022).

The most recent ctenochasmatids described from Cerro La Isla include a partial mandible with broken teeth (SGO.PV.347-c) and the posterior end of a mid-cervical vertebra (SGO.PV.22910; Alarcón-Muñoz et al., 2022). Alarcón-Muñoz et al. (2022) also figured and described the partial distal end of a right femur (SGO.PV.22913) which was regarded as an indeterminate pterodactyloid.

3.3.3. Rosablanca Formation, Colombia

At present, only fragmentary pterosaur remains have been reported from Colombia; specifically, material described by Cadena et al. (2020) from the upper Valanginian Rosablanca Formation. A partial left mandibular ramus (UR CP 0002), preserving Meckelian foramen was regarded as an ornithocheirid, whereas a fragmentary wing phalanx (UR CP 0003) was tentatively referred to the Ornithocheiroidea, based on the lenticular cross-sectional shape. The third specimen figured and described by Cadena et al. (2020) was regarded as a proximal end of a left radius (UCMP V4426/38367), belonging to an indeterminate pterodactyloid.

3.3.4. Tacuarembó Formation, Uruguay

At present, the only pterosaur remains reported from the Kimmeridgian–Hauterivian (Perea et al., 2009) Tacuarembó Formation of Uruguay are gnathosaurines (Perea et al., 2018), including *Tacuadactylus luciae* (Soto et al., 2021). Together, these remains confer a Late Jurassic age for the stratigraphic horizon from which they derive (Perea et al., 2018; Soto et al., 2021). The first pterosaur material reported from Uruguay was a fragmentary skull midsection (FC-DPV 3090) and six isolated teeth described and figured by Perea et al. (2018). Referral of FC-DPV 3090 to the Gnathosaurinae is supported by the rostrum being narrow and dorsoventrally compressed, with anterolaterally positioned maxillary teeth along the lateral margins of the jaws (Perea et al., 2018). The *Tacuadactylus luciae* holotype consists of a fragmentary rostrum (FC-DPV 2869) collected at the Batoví Quarry, whereas the referred specimens comprise dentary fragments from the Bidegain Quarry (FC-DPV 3415) and two isolated teeth (FC-DPV 3416; Soto et al., 2021). Referral to *Tacuadactylus* is supported by the presence of a dorsoventrally short, spatulate rostrum (Soto et al., 2021). Although there is no anatomical overlap between the rostra of FC-DPV 2869 and FC-DPV 3415, Soto et al. (2021) argued that the alveolar arrangement in both specimens was similar. Moreover, the two teeth (both FC-DPV 3416) associated with FC-DPV 3415 are similar in terms of cross-sectional shape and curvature to that of the holotype specimen (Soto et al., 2021). Based on the holotype and paratype specimens, *Tacuadactylus* tooth density varies between 1.58 and 2 teeth/cm, with teeth more densely packed in the anterior portion of the rostrum (Soto et al., 2021). The lateral margins of the rostrum in *Tacuadactylus* are scalloped because of inflation of the alveolar borders, as in *Plataleorhynchus* and *Gnathosaurus*, indicating a close relationship between these taxa (Soto et al., 2021).

3.3.5. Totoralillo Formation, Chile

Putative remains of a large pterosaur were reported from the Quebrada Los Cóndores (Totoralillo Formation) by Salinas et al. (1991). Based on ammonites recovered from the same stratigraphic horizon, these remains were interpreted as upper Hauterivian in age (Mourgues, 2004; Salinas et al., 1991); they still await formal description.

3.3.6. La Amarga Formation, Argentina

Despite hosting an abundant and diverse sauropod assemblage (Apesteguía, 2007) very little is known about pterosaurs from the Barremian La Amarga Formation (Neuquén Province, Argentina). An incomplete femur (MACN-N 02) was reported by Montanelli (1987) and interpreted as an indeterminate pterodactyloid. Montanelli (1987) noted that MACN-N 02 compares favourably with *Herbstosaurus*; however, they differ in terms of the medial deflection of the femoral head and the latter is slightly more robust. Given that there is some general disagreement surrounding the taxonomic placement of *Herbstosaurus* (see above), we follow Montanelli (1987) and regard MACN-N 02 as an indeterminate pterodactyloid.

3.3.7. Río Belgrano Formation, Argentina

At present, only appendicular elements have been reported from the Río Belgrano Formation in the Santa Cruz province of Argentina. A partial left ulna and what has been tentatively identified as a fourth wing metacarpal (both MACN-SC 3617). Although these were reported in association with ammonoids, conferring a Barremian age (Kellner et al., 2003), recent analysis of zircons indicate that the Río Belgrano Formation is Aptian in age (Ronda et al., 2022). Codorniú and Gasparini (2007) and Codorniú and Gianechini (2016) noted that the ulna and metacarpal appear to be from two different individuals, because of size incongruence. The ulna bears a well-developed ventral ridge near its proximal articulation, and on this basis was tentatively referred to the Ornithocheiridae (Kellner et al., 2003). However, as previously noted by Wellnhofer (1978), limb elements rarely possess diagnostic characters, even at low taxonomic levels. Possible exceptions include the deltopectoral crest of the humerus, and the thickness

of the cortical bone in the dsungaripteroids (character 58 of Unwin, 2003).

3.3.8. La Cruz Formation, Argentina

Pterosaur remains were first reported from the Aptian La Cruz Formation by Bonaparte and Sánchez (1975) who described a three-dimensionally preserved tibia and fused fibula and erected the taxon *Puntanipterus globosus* (FML 3869). This specimen was subsequently regarded as a dsungaripterid by Galton (1980), based on comparisons with '*Pterodactylus brancai*' from the Tendaguru Formation (HMN Nr. 2; HMN Nr. 6; BMNH R9191) and *Dsungaripterus weii*. Although the specimen was previously synonymised with *Pterodaustro guinazui* (Chiappe et al., 1998b; Codorniú and Gasparini, 2007; Dávila et al., 1999), other workers maintain that it is a dsungaripterid and a valid taxon (Bertozzo et al., 2021; Ji, 2020; Lü et al., 2009; Wellnhofer, 1991b).

3.3.9. Apón Formation, Venezuela

A left scapulocoracoid (MBLUZ P-911) derived from the Aptian Apón Formation constitutes the only pterosaur material reported from Venezuela and was tentatively referred to the Ornithocheiridae (Kellner and Moody, 2003). Although the specimen is three-dimensional, it is poorly preserved.

3.3.10. Araripe Basin, Brazil

The most significant South American pterosaur localities are the Lower Cretaceous Santana and Crato lagerstätten of Brazil, which have yielded diverse and abundant pterosaur remains. Exceptional preservation of soft tissues provides rare insights into particular aspects of pterosaur anatomy, as exemplified by the cranial crests of tapejarids (Campos and Kellner, 1997; Campos et al., 2017; Frey et al., 2003b), the wing membrane (Campos et al., 1984; Frey and Martill, 1994; Frey et al., 2003c), and brachiopatagium (Frey et al., 2003c; Kellner, 2004; Martill and Unwin, 1989). The former sheds light on the extremes of pterosaur cranial anatomy and evokes discussions regarding pterosaurian display, whereas the latter more accurately constrains the aerodynamics of flight. The discussion below, regarding the pterosaur material from the Araripe Basin (Fig. 1), follows the geologic nomenclature of Valença et al. (2003), wherein the Santana Formation was elevated to group status, and follows Beurlen (1963) in referring to the Crato Member as the Crato Formation.

The Crato Formation. The depositional environment of the Aptian Crato Formation has been interpreted as a restricted lagoon or lacustrine environment, with brackish, oxygenated surface waters and anoxic bottom waters (Heimhofer et al., 2010; Martill and Heimhofer, 2007; Valença et al., 2003). Despite some disagreement, most authors suggest deposition took place during the Aptian on the basis of palynological data (Frey et al., 2003a; Martill et al., 2007; Melo et al., 2020; Pons et al., 1990), with sedimentary and microfossil data indicating marine and fluvial influences, as well as strong seasonal variation (Leal et al., 2017). This unique combination of environmental factors has led to the exceptional preservation of fossil remains in laminated limestones (Martill et al., 1993).

Arthurdactylus conandoylei (SMNK PAL 1132) was the first pterosaur taxon described from the Crato Formation (Frey and Martill, 1994). The holotype specimen consists of a partially articulated skeleton missing the skull, cervical vertebrae and sternum and was most likely derived from the basal Nova Olinda Member (Frey and Martill, 1994). Appendicular elements include the left wing in articulation, the right wing and partial right hind limb (Frey and Martill, 1994). The skeleton has been laterally compressed and is preserved on a slab, limiting comparisons with three-dimensionally preserved ornithocheirid remains from the Santana Group. Nevertheless, *Arthurdactylus* represents one of the most complete postcranial ornithocheirids from the Araripe Basin, with an estimated wingspan of 4.6 m (Frey and Martill, 1994). Comparisons with other pterosaurs from the Cretaceous of South America are limited by the absence of cranial material; nevertheless, *Arthurdactylus* was distinguished from all other taxa based on its unique pelvis morphology and proportions of wing elements (Frey and Martill, 1994).

A partial skull, preserving the anterior end of the premaxilla–maxilla and mandibular symphysis with *in situ* teeth (MN 4797-V), was assigned to *Brasileodactylus* sp. by Sayão and Kellner (2000) based on the presence of a mandibular groove. However, this feature has been widely observed in ornithocheirid pterosaurs such as '*Tropeognathus robustus*' (Veldmeijer et al., 2005b), as well as the more distantly related targaryendraconians (wherein the mandibular groove is elevated relative to the tooth row; Pêgas et al., 2019). Referral of MN 4797-V to *Brasileodactylus* was supported by Veldmeijer (2003a) who regarded the specimen as *Brasileodactylus*. cf. *araripensis*, although they noted that despite the similarity in alveoli pattern, the dentition varied less in the holotype specimen. Subsequently, Veldmeijer et al. (2005b) noted that the dental pattern of MN 4797-V differed from *Brasileodactylus*, indicating that further comparisons with *Anhanguera* and *Tropeognathus* were required to elucidate the taxonomic significance of the dental synapomorphies of these taxa. The referral of MN 4797-V to *Brasileodactylus* is widely accepted, with the specimen regarded as *Brasileodactylus* indet. by Unwin and Martill (2007), *Brasileodactylus* cf. *araripensis* by Elias et al. (2007), and *Brasileodactylus araripensis* by Elgin and Frey (2011a).

The other ornithocheirid known exclusively from the Crato Formation is *Ludodactylus sibbicki* (SMNK PAL 3828). The holotype and only known specimen constitutes an almost complete skull preserved on a limestone slab (Frey et al., 2003a). The skull is preserved in right lateral view, with many elements still in articulation; the teeth are preserved in their alveoli, but the hyoids have been dislodged from their natural position and are observed in ventral view (Frey et al., 2003a). *Ludodactylus* was referred to the Ornithocheiridae on the basis of the third and fourth anterior teeth being the largest, but it lacks the distinctive premaxillary crest of the Ornithocheiridae; instead, it possesses a distinct parieto-occipital crest (Frey et al., 2003a). Unfortunately, the dorsal extent of this crest cannot be determined, as the portion of limestone which preserved this structure was erroneously removed prior to preparation of the specimen with pneumatic tools (Frey et al., 2003a). The only other ornithocheirid that possesses a similar parieto-occipital crest is *Caulkicephalus trimicrodon* from the Barremian Wessex Formation on the Isle of Wight, England (Steel et al., 2005). The holotype of *Ludodactylus sibbicki* is unique in that plant material is seemingly lodged between the mandibular rami, which the authors speculated as a possible cause of death (Frey et al., 2003a). As noted by Frey et al. (2003a), the discovery of more complete ornithocheirid remains from the Crato Formation will elucidate whether *Ludodactylus* might be referrable to *Arthurdactylus conandoylei* or represents a separate taxon. Additional material might also shed light on the whether ontogeny influences the morphology of the unique parieto-occipital crest of *Ludodactylus*. Phylogenetic analyses have indicated that *Ludodactylus* is closely related to *Guidraco venator* (Albian Jiufotang Formation) and *Caulkicephalus*, with the three forming a polytomy (Holgado and Pêgas, 2020; Pentland et al., 2022a). Alternatively, *Ludodactylus* and *Brasileodactylus* are recovered as sister taxa (Pentland et al., 2019).

Indeterminate ornithocheirids reported from the Crato Formation include an isolated tooth (MN 4798-V; Sayão and Kellner, 2000; Unwin and Martill, 2007), a near complete postcranial skeleton (SMNK PAL 3854; Elgin and Frey, 2012), and incomplete wings (MPSC R-739 and MPSC R-779) which were originally interpreted as tapejarids by Nuvens et al. (2002) but were later regarded as

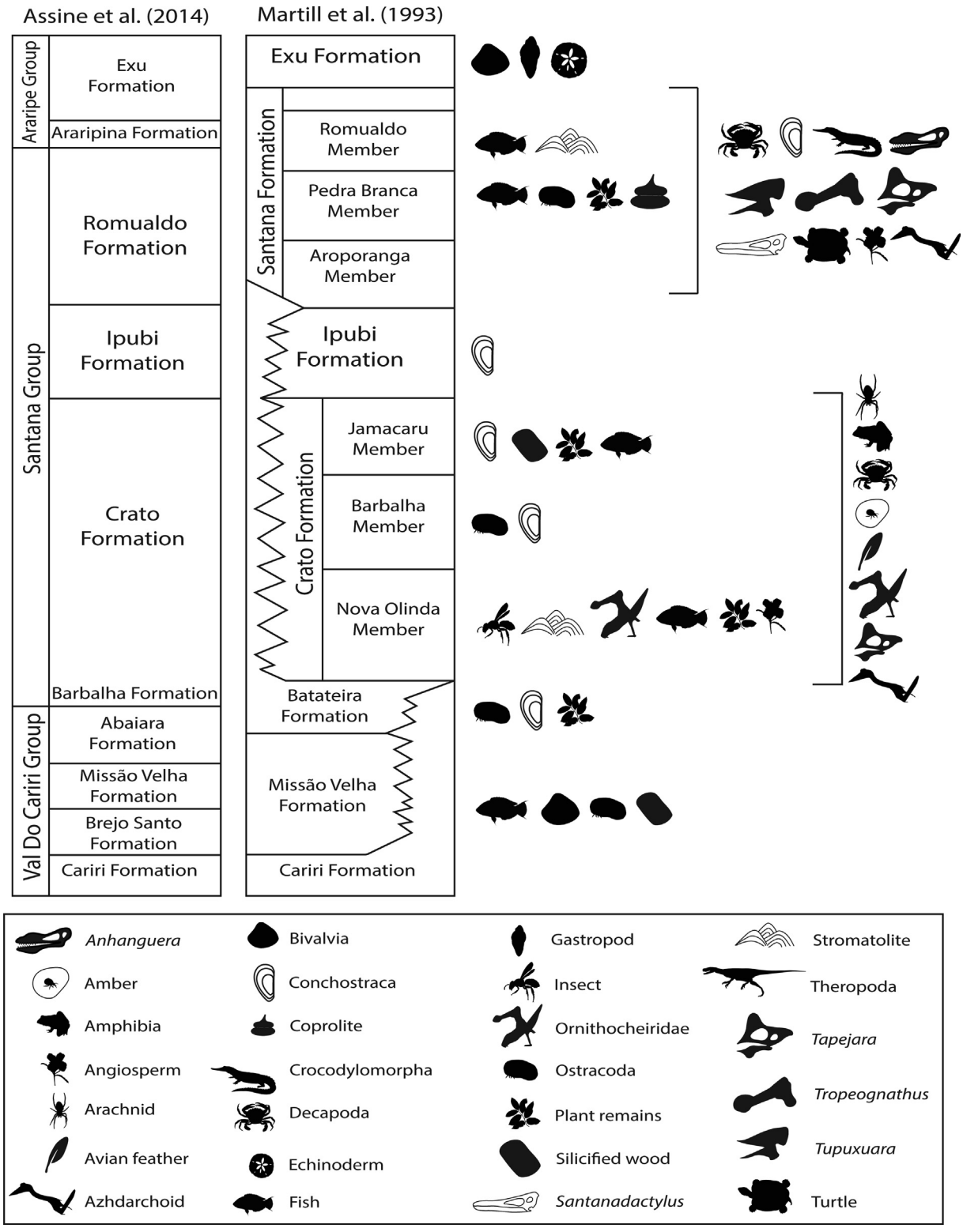

Fig. 1. Comparisons of the stratigraphic nomenclature of the Araripe Basin. Fossil occurrences pertain to the generalised stratigraphy proposed by Martill et al. (1993). *Anhanguera* and Ornithocheiridae redrawn from Wellnhofer (1991a), Conchostraca redrawn from Kozur and Weems (2010), *Santanadactylus* and *Tropeognathus* redrawn from Wellnhofer (1991c), *Tapejara* redrawn from Wellnhofer and Kellner (1991), *Tupuxuara* redrawn from Witton (2009). Silhouettes used herein by Birgit Lang (amber, arachnid), Nobu Tamura and T. Michael Keesey (amphibia), Daniel J. Bruzzese (angiosperm), Scott Hartman (Azhdarchoid), Katie S. Collins (Bivalvia), Smokeybjb (crocodylomorpha; vectorised by T. Michael Keesey), Hans Hillewaert (decapoda; vectorised by T. Michael Keesey), Michelle Site (echinoderm), Kent Sorgon (fish), Trond R. Oskars (gastropod), Melissa Broussard (insect) Robert Gay (ostracod), Falconaumanni and T. Michael Keesey (silicified wood), Oscar Alcober and Ricardo Martinez (theropoda) Roberto Díaz Sibaja (turtle), Silhouettes were downloaded from Phylopic (https://phylopic.org/) and are used under a Creative Commons Attribution-NonCommercial-ShareAlike 3.0 Unported Licence (https://creativecommons.org/licenses/by-nc-sa/3.0/). All other silhouettes drafted by A.H.P.

subadult ornithocheirids by Unwin and Martill (2007). Both partial wings have yet to be formally described. Although SMNK PAL 3854 differs from *Arthurdactylus* based on biometric ratios, without cranial material from either it cannot be determined whether these differences are of taxonomic significance (Elgin and Frey, 2012). Moreover, because of a lack of overlapping material, it cannot be determined whether SMNK PAL 3854 can be referred to *Ludodactylus*. More recently, Aureliano et al. (2014) referred SMNK PAL 3854 to *Arthurdactylus*, but did not provide any justification for this referral. Although Elgin and Frey (2012) did not include a detailed photograph of the pelvic girdle, based on their interpretative line drawing the ischiopubic plate differs from that of *Arthurdactylus conandoylei*, *Anhanguera santanae* and *Tropeognathus robustus*. However, it is also possible that the morphology of the pelvis, particularly the ischiopubic plate, has been altered because of taphonomic processes.

The first edentulous pterosaur described from the Crato Formation was *Tupandactylus imperator* (MCT 1622-R), which was based on a complete skull bearing a sagittal crest comprising a dorsally elongate ossified extension of the premaxilla (=bony crista) and suprapremaxillary spine which supported associated soft tissue (Campos and Kellner, 1997). The counterpart slab pertaining to the holotype specimen was recently described by Campos and Kischlat (2020), indicating the preservation of additional soft tissue. The spine constitutes the majority of the cranial crest and is more than 80% the total lateral area of the skull (Campos and Kellner, 1997). Moreover, the posterior portion of this crest extends beyond the occipital region of the skull (Campos and Kellner, 1997). The inferred primary function of this structure is for display; however, it is likely given its size and position to have influenced the aerodynamics (Campos and Kellner, 1997). The holotype specimen, MCT 1622-R was regarded by Campos and Kellner (1997) as an adult because of the complete fusion of the cranial elements. Originally described by Campos and Kellner (1997) as *Tapejara imperator*, the authors noted that the concave rostrum and comparatively large nasoantorbital fenestra were similar to those observed in *Tapejara wellnhoferi* from the Santana Group. Kellner et al. (2007a) subsequently allocated *Tapejara imperator* to the newly erected genus *Tupandactylus*, providing a revised diagnosis for this taxon. As noted by Kellner et al. (2007a), such nomenclatural acts were supported by the phylogenetic analysis of Martill and Naish (2006), in which they resolved a paraphyletic *Tapejara*. *Tupandactylus imperator* was regarded as its own species, primarily based on its larger size and distinct premaxillary crest, as well as a large nasoantorbital fenestra when compared with *Tapejara wellnhoferi* (Campos and Kellner, 1997). More recently, Pinheiro et al. (2012) figured and described a specimen referred to *Tupandactylus imperator* (CPCA 3590) comprising a partial skull with associated fossilised bacterial biofilm.

The second tapejarid taxon described from the Nova Olinda Member of the Crato Formation (also originally assigned to the genus *Tapejara*) is *Tupandactylus navigans* (SMNK PAL 2344; Frey et al., 2003b) comprising a near-complete cranium and associated soft tissue crest. This taxon was relocated to the newly erected genus *Tupandactylus*, along with *Tupandactylus imperator* by Kellner et al. (2007a). Although Frey et al. (2003b) described a second specimen of *Tupandactylus navigans* in their original report, both the holotype SMNK PAL 2344 and referred specimen SMNK PAL 2343 are missing the lower jaw. Despite this, excellent preservation of the cranial crest in both SMNK PAL 2344 and SMNK PAL 2343 permits the identification of an associated bony crista in addition to a keratinous extension of the premaxilla (Frey et al., 2003b). By contrast, an associated bony crista was not observed in *Tupandactylus imperator*; however, the apparent absence of this structure might be the result of taphonomic biases and might not be of taxonomic significance. Kellner et al. (2007a) noted that the posterior portion of the cranial crest is incompletely preserved in both the holotype and referred specimen, postulating that *Tupandactylus navigans* may in fact represent a junior synonym of *Tupandactylus imperator*. Despite this assertion, *Tupandactylus navigans* has been maintained as a valid taxon, with its inclusion in the phylogenetic analyses of Andres et al. (2014). The phylogenetic scores of this taxon have been refined with the description of a near-complete, articulated skeleton referred to *Tupandactylus imperator* (GP/2E 9266; Beccari et al., 2021). As in the holotype specimen of *Tupandactylus imperator* (SMNK PAL 2344), the referred specimen (GP/2E 9266) preserves soft tissue associated with an elongate suprapremaxillary spine.

The third edentulous pterosaur taxon from the Nova Olinda Member (Crato Formation, Araripe Basin) is *Caupedactylus ybaka* (MN 4726-V), which was described by Kellner (2013). The holotype specimen comprises a partial skull, a mandibular symphysis, and a partial right wing. The *Caupedactylus ybaka* holotype differs from other pterosaur specimens collected from the Crato Formation, in that it is three-dimensionally preserved (Kellner, 2013). Appendicular elements preserved in the holotype specimen include a complete scapulocoracoid, humerus and the proximal end of the first wing phalanx (Kellner, 2013). Based on complete fusion of the extensor tendon process, with no discernible sutures, as well as fusion of cranial elements, it is likely that MN 4726-V represents an adult individual (Kellner, 2013). *Caupedactylus* differs from other tapejarids, based on the morphology of the premaxillary sagittal crest, presence of slit-like fenestra on the palate, as well as the angle of the lacrimal process of the jugal (Kellner, 2013). The quadratojugal (firmly fused to the jugal and quadrate) is unusually thick and characterised by a rugose texture as well as small foramina, which was interpreted by Kellner (2013) as being pathological. In a recent phylogenetic analysis conducted by Kellner et al. (2019c), *Caupedactylus* was resolved in the most basal position within Tapejarinae.

Pêgas et al. (2016) described a fourth tapejarid taxon from the Crato Formation, *Aymberedactylus cearensis* (MN 7596-V), based on an almost complete mandible, missing part of the dentary crest and the left retroarticular process. Unlike most other pterosaur remains reported from the Crato Formation, the holotype specimen of *Aymberedactylus* is three-dimensionally preserved (Pêgas et al., 2016). *Aymberedactylus* differs from other tapejarids in that the retroarticular process is unusually elongate, and a shallow fossa was observed on the splenial which bears a distinct rugose texture (Pêgas et al., 2016). The presence of a shallow mandibular crest and mandibular symphysis equal to approximately half the total length of the mandible were regarded as tapejarine characteristics (Pêgas et al., 2016). *Aymberedactylus* and *Caupedactylus* both lack the step-like dorsal margin of the mandibular symphysis observed in some tapejarids (Kellner et al., 2019c; Pêgas et al., 2016).

In addition to the named tapejarids *Tupandactylus imperator*, *Tupandactylus navigans*, *Caupedactylus ybaka* and *Aymberedactylus cearensis*, indeterminate tapejarid remains have also been reported from the Crato Formation. Many of these were figured but not described by Unwin and Martill (2007), including a partial postcranial skeleton (MN 6527-V), partial wing and hind limb (MPSC R-771), partial postcranial skeleton (MPSC R-868), disarticulated partial wing and articulated hind limb (SMNK PAL 3830), and a partial postcranial skeleton (SMNK PAL 2342). Although Unwin and Martill (2007) provisionally regarded an incomplete postcranial skeleton (SMNK PAL 3900) as an indeterminate tapejarid, more recently it has been regarded as an indeterminate azhdarchoid (Eck et al., 2011; Elgin and Hone, 2013). The same is true of MN 4729-V, a complete left wing with preserved soft tissues that was briefly described as a tapejarid by Sayão and Kellner (1998). By contrast, Unwin and Martill (2007) regarded MN 4729-V as an indeterminate azhdarchoid, based on the wing proportions (first

wing phalanx more than 40% the total length of the wing finger, with the wing finger only 55% the total length of the forelimb). Conversely, a disarticulated postcranial skeleton (SMNK PAL 6409) which was provisionally regarded as an indeterminate azhdarchoid by Unwin and Martill (2007) has more recently been referred to the Tapejaridae by Elgin and Frey (2011b). A partial postcranial skeleton (SMNK PAL 3855) comprising articulated hind limb and near-complete wing was mentioned by Frey et al. (2003c) and Unwin and Martill (2007) but has yet to be formally described. Unwin and Martill (2007) regarded SMNK PAL 3855 as a tapejarid, based on comparisons with the biometric ratios of MN 4729-V.

The most recent edentulous pterosaur recognised from the Nova Olinda Member, *Lacusovagus magnificens* (SMNK PAL 4325; Witton, 2008), was established based on a partial skull. *Lacusovagus* was originally assigned to the Azhdarchidae on the basis of its narrow elongate edentulous jaw and large nasoantorbital fenestra, but differs from other members of this clade as its rostrum is relatively short and shallow, and lacks a crest (Witton, 2008). In a subsequent phylogenetic analysis conducted by Wu et al. (2017), *Lacusovagus* was recovered within the Thalassodromidae; however, another phylogenetic analysis by Leal et al. (2017) saw *Lacusovagus* tentatively resolved within Chaoyangopteridae. Cerqueira et al. (2021) also regarded *Lacusovagus* as a putative chaoyangopterid; however, based on the phylogenetic analysis presented by Andres (2021) *Lacusovagus* is a member of the Tapejaridae.

Indeterminate pterosaur remains mentioned but not described from the Crato Formation include a partial wing (SMNK PAL 3842; Unwin and Martill, 2007), as well as a humerus (MPSC R-869), partial skull (MPSC R-931) and partial postcranial skeleton with associated soft tissue preservation (MPSC R-932) mentioned by Sayão and Kellner (2000), Nuvens et al. (2002) and Unwin and Martill (2007).

3.3.11. The Santana Group, Brazil

The richest and most speciose pterosaur assemblage from Gondwanan is undoubtedly the Aptian–lower Albian Santana Group deposited within the Araripe Basin in north-eastern Brazil (Assine et al., 2014; Martill, 1993). Fossils derived from the Romualdo Formation of the Santana Group are often preserved three-dimensionally within calcareous nodules (Wellnhofer, 1991c), whereas pterosaurs from the Crato Formation are preserved in laminated limestones and often crushed as a result of lithostatic pressure (Martill et al., 1993). Before the first pterosaur remains were reported from the lagerstätten of the Romualdo Formation by Price (1971), this stratigraphic horizon was predominantly known for yielding many different species of fish (Brito and Yabumoto, 2011; Martill, 1988). The assemblage is dominated by ornithocheirids (Bantim et al., 2014; Kellner and Tomida, 2000; Pinheiro and Rodrigues, 2017; Vila Nova et al., 2014; Wellnhofer, 1985; Wellnhofer, 1991a), with tapejarids (Eck et al., 2011; Elgin and Campos, 2012; Wellnhofer and Kellner, 1991), and thalassodromids also present (Kellner et al., 1988; Kellner et al., 1994; Kellner et al., 2002; Veldmeijer et al., 2005b; Witton, 2009).

The publication of many new species of ornithocheirids from the Santana Group during the late 20th Century expedited our understanding of pterosaurs from South America (Campos and Kellner, 1985a; De Buisonjé, 1981; Wellnhofer, 1985, 1987; Wellnhofer, 1991a; Wellnhofer, 1991c). Although considerably less controversial than the taxonomy of the fragmentary ornithocheirids from the Cambridge Greensand (Rodrigues and Kellner, 2013), competing taxonomic proposals have been presented. While some taxa have been regarded as junior synonyms, or regarded as indeterminate ornithocheirids owing to a lack of diagnostic features, the taxonomic position of some specimens remains contentious. Fortunately, almost all taxa described from the Santana Group have been established based on cranial, or partial cranial material, enabling direct comparison between overlapping material.

Perhaps the most speciose genus of Gondwanan pterosaur is *Anhanguera*, with as many as six species allocated to this genus at one time (Pinheiro and Rodrigues, 2017). A detailed revision of the taxonomy of *Anhanguera* was provided by Pinheiro and Rodrigues (2017), who regarded '*Anhanguera santanae*' (BSP 1982 I 90; Wellnhofer, 1985), '*Anhanguera araripensis*' (BSP 1982 I 89; Wellnhofer, 1985) and '*Anhanguera robustus*' (BSP 1982 I 47; Wellnhofer, 1987b) as *nomina dubia*. Following those authors, three species of *Anhanguera* are considered valid: *Anhanguera blittersdorffi* (MN 4805–V; Campos and Kellner, 1985a); *Anhanguera piscator* (NSM-PV 19892; Kellner and Tomida, 2000); and *Anhanguera spielbergi* (RGM 401 880; Veldmeijer, 2003a). Pinheiro and Rodrigues (2017) also provided a revised diagnosis for *Anhanguera*, excluding characters that vary during ontogeny and those that are widespread within ornithocheirids. These authors also reported that the premaxillary crest in *Anhanguera* demonstrates positive allometric growth, and thus the dorsoventral height and anterior extent of the crest is not diagnostic at species-level (Pinheiro and Rodrigues, 2017). Pinheiro and Rodrigues (2017) also noted that members of this clade possess a parietal crest, moderate palatal ridge, and the 5th and 6th maxillary teeth are smaller than the 4th and 7th. Pinheiro and Rodrigues (2017) noted that while some ornithocheirids from the Romualdo Formation might in fact represent anagenetic morphotypes, a lack of precise stratigraphic data for many taxa precludes testing of this hypothesis.

Anhanguera blittersdorffi (sometimes misspelled '*Anhanguera blittersdorfi*') was first described by Campos and Kellner (1985b), with the holotype specimen, MN 4805-V (previously CD-R-001) comprising a complete skull. A second specimen, preserving a skull and mandible (Pz-DBAVUERJ n. 40a, also referred to as n. 40 Pz-DBAV-UERJ or Pz-DBAVUERJ n. 40) was figured by Kellner and Hasegawa (1993) and Kellner and Tomida (2000); however, the specimen has not been formally described. When the holotype specimen was initially described, the diagnosis presented by Campos and Kellner (1985b) for *Anhanguera blittersdorffi* pertained to the specific, generic, and family levels, as this taxon was the first member of the Anhangueridae. Kellner and Tomida (2000) later provided an emended diagnosis for the species, regarding many of the autapomorphies of *Anhanguera blittersdorffi* as synapomorphies present in other related taxa. *Anhanguera blittersdorffi* differs from other ornithocheirids in that the skull is dorsoventrally shorter; in addition, the quadrate is proportionally shorter when compared with *Anhanguera piscator* (Kellner and Tomida, 2000). Kellner and Tomida (2000) estimated that *Anhanguera blittersdorffi* possesses 52 teeth in the upper jaw, contrasting with '*Anhanguera santanae*', which has approximately 40 teeth in the premaxilla–maxilla. Although Kellner and Tomida (2000) noted that *Anhanguera blittersdorffi* differs from other members of this genus in terms of the morphology of the premaxillary crest, more recent analyses utilising geometric morphometrics by Pinheiro and Rodrigues (2017) indicate that premaxillary crests are allometrically correlated with skull size. As such, the number of teeth present in the upper jaw is perhaps the most reliable autapomorphy of *Anhanguera blittersdorffi* (Pinheiro and Rodrigues, 2017). Both the holotype and referred specimen of *Anhanguera blittersdorffi* are known only from cranial material (Kellner, 1996); no other material has been referred to this taxon.

Anhanguera piscator (NSM-PV 19892) was erected by Kellner and Tomida (2000) based on a complete skull and mandible preserving *in situ* teeth, associated with a partial postcranial skeleton. Postcranial elements include: cervical, dorsal, sacral and caudal vertebrae; pectoral girdle represented by the sternum and scapulocoracoid; pelvic girdle; and appendicular elements including wing bones and part of the hind limb (Kellner and Tomida, 2000). The

specimen was collected from the Santana do Cariri (Ceara, north-eastern Brazil) and is three-dimensionally preserved; however, some elements of the skull have been dislodged from their original positions (Kellner and Tomida, 2000). This is primarily because several elements in the *Anhanguera piscator* holotype specimen are unfused, indicating that the individual was not osteologically mature (Kellner and Tomida, 2000). Although the sacral neural arches are fused to their respective sacral vertebrae, the sacral vertebrae are preserved together but not fused along their centra (Kellner and Tomida, 2000). Despite the immaturity of the holotype specimen, Kellner and Tomida (2000) estimate based on the preserved wing elements that the wingspan was approximately 5 m. As in *Anhanguera blittersdorffi*, the posteriormost dental alveoli of *Anhanguera piscator* are positioned near the midpoint of the nasoantorbital fenestra (Campos and Kellner, 1985b); however, the tooth count varies, with the latter possessing 50 teeth in the premaxilla–maxilla (Kellner and Tomida, 2000). By contrast, the lower jaw possessed 37 teeth, with 19 alveoli preserved on the left and 18 on the right (Kellner and Tomida, 2000). *Anhanguera piscator* was distinguished from other ornithocheirids based on the morphology of its premaxillary crest (Kellner and Tomida, 2000); however, it remains uncertain as to how the crest varies during ontogeny. This interpretation was supported by Pinheiro and Rodrigues (2017) who noted that the dorsoventral height of the premaxillary crest in *Anhanguera piscator* cannot be solely explained by allometric growth, and thus differs from other ornithocheirids. Pinheiro and Rodrigues (2017) also noted that *Anhanguera piscator* differs from related taxa, based on the morphology of the basisphenoid.

Anhanguera spielbergi (originally described as 'Coloborhynchus spielbergi'; Veldmeijer, 2003a) was established based on a partial skull and mandible, and postcranial elements (RGM 401 880). The postcranial skeleton is represented by cervical vertebrae VIII and IX, dorsal vertebrae VI–XII, five dorsal ribs, pectoral and pelvic girdle, elements from the left wing and parts of both hind limbs (Veldmeijer, 2003a). As with other ornithocheirids described from the Romualdo Formation of the Araripe Basin, the precise locality from whence the holotype specimen derives remains unknown (Veldmeijer, 2003a). As in other species of *Anhanguera*, the anterior portion of the skull is laterally expanded, but the mandibular groove encroaches upon this expansion (Veldmeijer, 2003a). Although Pinheiro and Rodrigues (2017) considered *Anhanguera spielbergi* as valid, they noted that several diagnostic characters mentioned by Veldmeijer (2003a) might be influenced by ontogeny, whereas others are local synapomorphies within Ornithocheiridae. This includes the weakly defined palatal ridge, medially deflected mandibular rami and the morphology of the premaxillary crest (Pinheiro and Rodrigues, 2017). Although the total number of teeth present in the skull cannot be determined with certainty, Veldmeijer (2003a) estimated that each side possesses 19 alveoli. Thus, the number of alveoli present in *Anhanguera spielbergi* is slightly higher than *Cearadactylus atrox* but might be lower than *Anhanguera blittersdorffi* (Veldmeijer, 2003a).

'*Anhanguera santanae*' (originally described as *Araripesaurus santanae*; Wellnhofer, 1985) was established based on BSP 1982 I 90, a partial skull associated with elements from the right wing. The skull and mandible are both missing their anterior end; however, the occipital region is preserved (Wellnhofer, 1985). Postcranial elements preserved in BSP 1982 I 90 include the right ulna, radius, proximal and distal carpals and the proximal end of metacarpal IV. Other material referred to '*Araripesaurus*' or '*Anhanguera santanae*' includes a partial postcranial skeleton (BSP 1982 I 91) and a partial hind limb (BSP 1982 I 93; Wellnhofer, 1985). Wellnhofer (1991a) subsequently referred *Araripesaurus santanae* to *Anhanguera*, and described a partial skeleton including skull and fragmentary mandible (AMNH 22555) as a referred specimen of '*Anhanguera santanae*'. More recently, Pinheiro and Rodrigues (2017) noted several morphological differences between BSP 1982 I 90 and AMNH 22555, regarding the latter as *Anhanguera* sp.

'*Anhanguera araripensis*' (originally described as '*Santanadactylus araripensis*', sometimes misspelled '*Santandactylus*') was established based on BSP 1982 I 89, comprising the mid-section of the skull, partial hyoid, mandible predominantly comprising mandibular rami, isolated teeth and appendicular elements (Wellnhofer, 1985). All appendicular elements are from the right wing, including partial humerus, the distal ends of the ulna and radius, carpal elements, sesamoids of the carpus, and the proximal ends of metacarpals III and IV (Wellnhofer, 1985). A complete skull (MN 4735-V), was regarded as cf. '*Anhanguera araripensis*' by Kellner and Tomida (2000), based on the proximity of the premaxillary crest to the nasoantorbital fenestra, as well as the lateral deflection of the pterygoids. A complete skull lacking the mandible (SAO 16494) was mentioned by Veldmeijer (2003a) and Veldmeijer et al. (2005b), who regarded the specimen as '*Coloborhynchus araripensis*'; with the specimen briefly described by Veldmeijer et al. (2006). The referral of SAO 16494 to '*Coloborhynchus araripensis*' was largely based on position of the anteriormost premaxillary alveoli (Veldmeijer et al., 2006). By contrast, Barrett et al. (2008) regarded '*Santanadactylus araripensis*' as Pterodactyloidea *incertae sedis*, whereas Pinheiro and Rodrigues (2017) regarded '*Anhanguera araripensis*' as a *nomen dubium*, on the basis that the holotype specimen is non-diagnostic, and regarded both referred specimens (MN 4735-V and SAO 16494) as *Anhanguera* sp.

Other cranial remains referred to *Anhanguera* include a partial mandible (AMNH 22573) that was figured and mentioned by Veldmeijer (2003a). Although Veldmeijer (2003a) noted the dimensions of the dentary crest, AMNH 22573 awaits formal description. Other recent cranial material designated *Anhanguera* sp. includes the anterior portion of a rostrum (DGEO-CTG-UFPE 8283; Duque et al., 2022) lacking premaxillary crest. Referral of DGEO-CTG-UFPE 8283 to the genus *Anhanguera* is supported by the 5th and 6th pairs alveoli being smaller than the 4th and 7th (Duque et al., 2022).

SAO 200602 is known from an almost complete mandible with deep, blade-like dentary crest and *in situ* teeth, and was first mentioned and figured by Veldmeijer (2003a). A brief description of SAO 200602 was included by Veldmeijer et al. (2005b), who noted the presence of a mandibular groove; however, the full extent of this feature both anteriorly and posteriorly remains uncertain. As in most other ornithocheirids, the largest teeth are confined to the anteriormost section of the mandible, and the anterior portion of the mandible is laterally expanded (Kellner and Tomida, 2000; Veldmeijer et al., 2005b).

Yet more material referred to *Anhanguera* includes SMNK PAL 1136, which was figured by Frey and Martill (1994) and is known from a skull and mandible, pelvic and shoulder girdle, and elements from both wings. Frey and Martill (1994) included the lengths of the wing elements of SMNK PAL 1136, and compared these with the biometric ratios of *Arthurdactylus conandoylei*. Despite being represented by cranial and appendicular elements, SMNK PAL 1136 has yet to be formally described but has been regarded by Frey and Martill (1994) and Pinheiro and Rodrigues (2017) as *Anhanguera* sp.

Additional ornithocheirid remains include a skull and mandible (MN 6687-V), and skull (MN 6503-V) assigned to '*Coloborhynchus*' sp. (Veldmeijer et al., 2005a; Veldmeijer et al., 2006). These specimens await formal description.

Barbosania gracilirostris (MHNS/00/85; Elgin and Frey, 2011a) was established based on a partial skeleton preserving the skull and mandible, cervical vertebra IX, the notarium, elements from both the left and ring wing, and both femora. The holotype specimen is not osteologically mature, as the scapula and coracoid are

preserved as separate elements (Elgin and Frey, 2011a). Unlike most ornithocheirids reported from the Romualdo Formation, *Barbosania* lacks a premaxillary and dentary crest, with the absence of sagittal crests interpreted by Elgin and Frey (2011a) as taxonomically significant, rather than the result of ontogeny. These authors noted that cranial crests develop relatively early in ontogeny, with little evidence to suggest that putative females were completely crestless (Elgin and Frey, 2011a). It should be noted that although crests were noted in juveniles of the *Caiuajara dobruskii* (Manzig et al., 2014), juvenile and neonate ornithocheirid pterosaurs have not yet been reported. *Barbosania* differs from the other crestless ornithocheirids described from the Romualdo Formation, *Brasileodactylus*, because the first tooth pair on the premaxilla is procumbent (Elgin and Frey, 2011a). Recent phylogenetic analysis has resolved *Barbosania* in a polytomy with *Targaryendraco wiedenrothi* and *Aussiedraco molnari*; alternatively, *Barbosania* is placed in Targaryendraconia (Pêgas et al., 2019). Unfortunately, as the skull and mandible in *Barbosania* are preserved in occlusion with adherent matrix between these elements, it cannot be determined whether a bony bar separates the first mandibular tooth pair. Elgin and Frey (2011a) noted that there are approximately 48 alveoli in the upper jaw, and 40 alveoli in the lower jaw, considerably fewer than *Anhanguera blittersdorffi* and '*Anhanguera santanae*', which possess 52 and 40 teeth in the upper jaw respectively (Kellner and Tomida, 2000). By contrast, Wellnhofer (1987) noted that the upper jaw preserves 34 alveoli in *Tropeognathus mesembrinus*.

Brasileodactylus araripensis is a crestless ornithocheirid that was established on the basis of an anterior section of a mandible (MN 4804; Veldmeijer et al., 2009; italicise). Italicise diagnosed *Brasileodactylus araripensis* based on the presence of a procumbent first tooth pair in the mandible, and presence of a mandibular groove which becomes progressively wider posteriorly. A revised diagnosis of *Brasileodactylus araripensis* was provided by Veldmeijer et al. (2005b), who noted that this taxon differs from other ornithocheirids based on the positions of the first and second tooth pair of the mandible, and presence of laterally positioned grooves parallel to the mandibular groove. Veldmeijer (2003b) figured and described a skull, mandible and appendicular elements (AMNH 24444), regarding the material as *Brasileodactylus* sp. based on the absence of cranial sagittal crests. Although the cranial material in AMNH 24444 is disarticulated, several wing elements are articulated, including the distal end of the right ulna and radius with the carpal elements and metacarpals III and IV (Veldmeijer, 2003b). Unfortunately, AMNH 24444 has been prepared such that each element is visible in one view only, and thus comparisons with the *Brasileodactylus araripensis* holotype specimen are limited (Veldmeijer, 2003b; Veldmeijer et al., 2005b). A smaller, more complete mandible (SMNS 55414) was also referred to *Brasileodactylus* by Veldmeijer et al. (2005a) and Veldmeijer et al. (2009), based on the configuration of the alveoli, lateral expansion of the anterior end of the symphysis, and mandibular groove with parallel subgrooves. Veldmeijer et al. (2005a) also referred a specimen represented by a partial maxilla and skeleton (BSP 1991 I 27) to *Brasileodactylus* sp. based on the preserved alveoli. Another partial mandible (MN 6517-V), was regarded by Veldmeijer et al. (2005a) as *Brasileodactylus?araripensis* and awaits formal description.

One of the most recently named species of pterosaur from the Romualdo Formation is *Maaradactylus kellneri* (MPSC R 2357; Bantim et al., 2014), represented by a partial skull, the atlas, and the axis. The holotype specimen, MPSC R 2357, was found exposed at the surface and collected from Sítio São Gonçalo, near Santana do Cariri in northeastern Brazil (Bantim et al., 2014). The premaxillary crest of *Maaradactylus* is similar to that of *Tropeognathus mesembrinus*, and begins at the anterior end of the skull (Bantim et al., 2014). Both *Maaradactylus* and *Tropeognathus mesembrinus* also possess parietal crests; however, because of poor preservation of this part of the skull in *Maaradactylus*, it cannot be determined whether this structure posteriorly overhangs the occipital region as in *Tropeognathus mesembrinus* (Wellnhofer, 1987). The dentition of *Maaradactylus kellneri* differs from that of other ornithocheirids reported from the Romualdo Formation, with 70 alveoli preserved in the upper jaw, and the distal teeth (from the 18th to 35th tooth positions) occurring in sets of three or 'triplets' (Bantim et al., 2014). Phylogenetic analysis conducted by Bantim et al. (2014) utilising the dataset of Wang et al. (2009) resolved *Maaradactylus* and *Tropeognathus mesembrinus* as sister taxa, with that clade sister to the *Anhanguera*. By contrast, *Maaradactylus* has been more recently resolved as the sister taxon to *Cearadactylus atrox*, with *Maaradactylus* + *Cearadactylus* sister to *Anhanguera* (Holgado and Pêgas, 2020; Pêgas et al., 2019; Pentland et al., 2022a).

As with many pterosaurs described from the Araripe Basin, *Tropeognathus mesembrinus* and '*Tropeognathus robustus*' were collected from the "Chapada do Araripe", a plateau that borders the states of Ceara and Pernambuco, northeastern Brazil; however, the precise locality of the type material remains unknown (Wellnhofer, 1987). *Tropeognathus mesembrinus* (BSP 1987 I 46) was established based on a partial skull, whereas '*Tropeognathus robustus*' (BSP 1987 I 47) is based on a complete mandible (Wellnhofer, 1987). Both specimens are three-dimensionally preserved with minimal taphonomic distortion; however, the premaxilla in *Tropeognathus mesembrinus*, which forms the dorsal margin of the nasoantorbital fenestra, is somewhat depressed (Wellnhofer, 1987). Unfortunately, in the *Tropeognathus mesembrinus* type specimen, the right mandibular ramus is completely absent and the retroarticular process of the left ramus is missing (Wellnhofer, 1987). Moreover, *in situ* teeth in both specimens are largely confined to the anterior portions of each jaw, with the posteriormost alveoli unoccupied (Wellnhofer, 1987). *Tropeognathus mesembrinus* differs strongly from other ornithocheirid pterosaurs: its sagittal crests are confined to the anterior ends of the premaxilla and mandible; it has comparatively fewer teeth; it has a short, blunt parietal crest extending beyond the occiput; and the upper and lower jaws are not laterally expanded (Wellnhofer, 1987). Although Wellnhofer (1987) noted a mandibular groove and corresponding palatal ridge as potential autapomorphies of this taxon, this feature has now been found to be synapomorphic of the Anhangueria (see Rodrigues and Kellner, 2013). A more derived possible synapomorphy is the presence of a flattened, triangular area with medial depression dorsal to the first tooth pair (Wellnhofer, 1987). Jacobs et al. (2019) regarded this as an upturned, anteriorly positioned extension of the palatal surface (=deltoid facet), also present in *Siroccopteryx moroccensis* and some ornithocheirids. Given that recent phylogenetic analyses have demonstrated a close relationship between *Tropeognathus mesembrinus* and *Siroccopteryx moroccensis* (Holgado and Pêgas, 2020; Pentland et al., 2022a), the deltoid facet may be synapomorphic for this clade.

The '*Tropeognathus robustus*' holotype specimen comprises a complete mandible (BSP 1987 I 47); however, only the right ramus of '*Tropeognathus robustus*' was figured, as the left was still obscured by matrix from the limestone concretion (Wellnhofer, 1987). A second specimen (SMNK 2302 PAL) comprising the anterior end of an upper and lower jaw was subsequently referred to this taxon by Fastnacht (2001) as '*Coloborhynchus robustus*'. Other remains attributed to this taxon include a partial skeleton (SMNK PAL 1133) first mentioned by Frey and Martill (1994). Although the measurements of the appendicular elements and biometric ratios of SMNK PAL 1133 were given by Elgin and Frey (2012), this specimen awaits formal description. '*Tropeognathus robustus*' differs from *Tropeognathus mesembrinus* in terms of its dentition, interalveolar spacing, the morphology of the mandibular crest,

and the anterior end of the mandible in the former is laterally expanded (Wellnhofer, 1987). '*Tropeognathus robustus*' was subsequently referred to the genus *Anhanguera* by Kellner and Tomida (2000). By contrast, Fastnacht (2001) referred *Tropeognathus mesembrinus* to *Criorhynchus* and '*Tropeognathus robustus*' to *Coloborhynchus*, with the latter reassigned "since the diagnosis given by Wellnhofer (1987b) does not allow distinction of *Tropeognathus* from other pterosaur genera" (p. 35). Veldmeijer (2003a) maintained the referral of Fastnacht (2001) in which '*Tropeognathus robustus*' was regarded as '*Coloborhynchus robustus*', based on similarities between '*Coloborhynchus spielbergi*' (RGM 401 880) and SMNK 2302 PAL, the paratype of '*Coloborhynchus robustus*'. Pinheiro and Rodrigues (2017) regarded '*Anhanguera robustus*' as a *nomen dubium*, whereas many workers regard *Tropeognathus mesembrinus* as valid (Aires et al., 2021; Pinheiro et al., 2019; Rodrigues and Kellner, 2013). Although SMNK PAL 1133 was regarded by Elgin and Frey (2011a) as an ornithocheirid, the specimen has subsequently been reffered to '*Coloborhynchus robustus*' by Elgin and Frey (2012) and '*Anhanguera robustus*' by Aires et al., 2021.

To date, two specimens have been regarded as comparable to *Tropeognathus mesembrinus*: SMNS 56994, and MN 6594-V, each of which is three-dimensionally preserved. SMNS 56994 comprises a mandible with *in situ* teeth and was figured by Veldmeijer (2003a) as cf. *Tropeognathus mesembrinus* (Myers, 2010; Veldmeijer, 2003a; Veldmeijer et al., 2005a) but awaits formal description. Kellner et al. (2013) also briefly mentioned SMNS 56994, noting that the specimen had not been fully prepared. By contrast MN 6594-V comprises a partial skeleton, including cranial, axial and appendicular elements (Kellner et al., 2013). Unfortunately, some elements have been partially eroded, suggesting parts of the concretion surrounding this material had been exposed for some time (Kellner et al., 2013). Kellner et al. (2013) regarded MN 6594-V as *Tropeognathus* cf. *T. mesembrinus*, based on the presence of a low, blunt, sagittal premaxillary crest, relatively few teeth and inclined dorsal margin of the occipital region. As well as preserving part of the maxilla, including the anterior margin of the nasoantorbital fenestra and the posterior portion of the premaxillary crest, MN 6594-V preserves a braincase, jugal, quadrate and basisphenoid (Kellner et al., 2013). Although only a small portion of the premaxillary crest of MN 6594-V is preserved, Kellner et al. (2013) observed several shallow channels on the cortical bone, interpreting these as impressions from blood vessels. Kellner et al. (2013) noted these were similar to the structures observed in *Thalassodromeus sethi* by Kellner et al. (2002), speculating that these might have assisted in temperature regulation in both taxa. Referral of MN 6594-V to *Tropeognathus* is further supported by the presence of a frontoparietal crest, posteriorly overhanging the occiput region, as in the *Tropeognathus mesembrinus* holotype specimen. Based on the few alveoli preserved in the mandible, the spacing and number of teeth seems congruent with *Tropeognathus* and is lower when compared with *Anhanguera* (Kellner et al., 2013). The postcranial elements vary in terms of preservation, but compare favourably with other ornithocheirids (Kellner et al., 2013). The cervical series is represented by the posteriormost cervical vertebrae, with each possessing a laterally placed pneumatic foramen and tall neural spines, typical of ornithocheirid cervical vertebrae (Kellner et al., 2013). Twelve dorsal vertebrae were observed in MN 6594-V, with the first five fused together and forming the notarium; however, although all five are fused at their centra, some dorsal spines remain unfused (Kellner et al., 2013). Moreover, the first dorsal rib was associated but not fused to its corresponding vertebra (Kellner et al., 2013). Given that not all dorsal spines are fully fused in the notarium, Aires et al., 2021 regarded MN 6594-V as close to notarium stage 5 (NSF5), indicating these differences are reflective of these specimens being at different ontogenetic stages. The five sacral vertebrae of MN 6594-V are fully fused to the ilium, forming a synsacrum, with the third and fourth bearing keeled ventral surfaces and thus differing from other pterosaurs (Kellner et al., 2013). By contrast *Anhanguera piscator* possesses five sacral vertebrae, and *Anhanguera spielbergi* has six—with the last being a 'captured' caudal vertebra (Kellner et al., 2013). Other postcranial elements in MN 6594-V include both scapulocoracoids, partial sternum, partial humeri, partial radii, partial ulnae, carpal elements, metacarpals I-III, the distal end of the first wing phalanx, partial pelvis and femur (Kellner et al., 2013). Although several wing elements are incomplete, based on comparisons with *Anhanguera piscator* and AMNH 22552, the wingspan estimate varied between 8.26 and 8.70 m, making it one of the largest Gondwanan pterosaurs (Kellner et al., 2013).

One of the earliest reports of pterosaur cranial material preserved in limestone nodules was *Cearadactylus atrox* (MN 7019-V) which was mentioned by Leonardi and Borgomanero (1983) and described later described by Leonardi and Borgomanero (1985). At the time of its description, the holotype specimen (comprising a partial skull and lower jaws, preserved within a single nodule) was held in a private collection, and subsequently donated to the Museu Nacional/UFRJ (Vila Nova et al., 2014). As noted by Kellner and Tomida (2000), the right lateral surface of the skull is damaged, such that interpretations of some elements are provisional. *Cearadactylus atrox* was regarded as a pterodactyloid, supported by the presence of a confluent nasoantorbital fenestra (Leonardi and Borgomanero, 1985); however, Leonardi and Borgomanero (1983) first regarded it as a member of the Ornithocheiridae. The description of this specimen by Leonardi and Borgomanero (1985) was subsequently followed by disagreement regarding the taxonomic placement of this taxon (see Vila Nova et al., 2014). Wellnhofer (1991a) later reallocated *Cearadactylus atrox* to the newly erected clade 'Cearadactylidae', which was defined by extremely large rostral teeth, whereas Kellner and Tomida (2000) regarded *Cearadactylus atrox* as a pteranodontoid, based on laterally wide and spatulate morphology of the anterior end of the jaws. Unwin (2002) maintained that *Cearadactylus atrox* was a valid taxon, and placed it within the Ctenochasmatoidea, based on the results of a phylogenetic analysis. These results are largely based on the presence of the ctenochasmatoid synapomorphy "quadrate oriented in a subhorizontal position", or "high cheek" present in *Cearadactylus atrox*. The lack of consensus regarding the phylogenetic position of this specimen is unsurprising, since the original diagnosis for this taxon was unfortunately based on an artificially augmented partial skull (Vila Nova et al., 2014). Originally, the purported *Cearadactylus* holotype was regarded as a partial skull, represented by premaxilla–maxilla and dentary with *in situ* teeth, surangular, angular, articular and fused quadrate, quadratojugal and jugal (Leonardi and Borgomanero, 1985). When initially described, the upper and lower jaws were associated but separated by adherent limestone matrix (Leonardi and Borgomanero, 1985). Leonardi and Borgomanero (1985) noted that *Cearadactylus atrox* differed from other pterosaur material, in that the anterior teeth were distinctly large, the anterior ends of the jaws were spatulate and the jaws were agape, even when fully occluded. A number of characters upon which *Cearadactylus atrox* was originally diagnosed were later proven incorrect, after the holotype specimen was further prepared after its donation to the Museu Nacional (Vila Nova et al., 2014). Although the dorsal margin of the premaxilla–maxilla is incomplete in the holotype and only known specimen, Leonardi and Borgomanero (1985) regarded *Cearadactylus atrox* as a crestless pterosaur. Additional preparation of the holotype specimen revealed the vestiges of a sagittal crest from the anterior tip of the rostrum to at least the fifth maxillary alveolus (Vila Nova

et al., 2014), *contra* Leonardi and Borgomanero (1985). As noted by Vila Nova et al. (2014), many anatomical misinterpretations pertaining to *Cearadactylus atrox* are largely because the lower jaw was erroneously glued to the maxilla, and the premaxilla–maxilla attached to the dentary. Moreover, the enlarged teeth of the premaxilla were false and not representative of the true dental morphology (Martill, 2011; Vila Nova et al., 2014). A revised diagnosis of *Cearadactylus atrox* was presented by Vila Nova et al. (2014) noting that it is a valid taxon. More recent phylogenetic analyses resolve *Cearadactylus atrox* as the sister taxon to *Maaradactylus kellneri*, with *Cearadactylus atrox* + *Maaradactylus kellneri* sister to *Anhanguera* (Pentland et al., 2022a). The mandibular groove of *Cearadactylus atrox* is unique among ornithocheirids, in that it bifurcates near the anterior end of mandible. Although it is possible that the mandibular groove of *Aussiedraco molnari* also bifurcates, this cannot be determined as the *Aussiedraco* holotype specimen was potentially over prepared, with two sulci preserved on the anterior end of the occlusal surface. If *Aussiedraco* did possess a bifurcating mandibular groove, given that it is resolved within the Targaryendraconia, it is likely that *Cearadactylus* and *Aussiedraco* independently evolved a bifurcating mandibular groove.

The taxonomic validity of?*Cearadactylus ligabuei* (CSRL 12,692 / 12713) is dubious. The holotype and only known specimen was first described by Dalla Vecchia (1993) and comprises a partial skull, preserving the premaxilla–maxilla, left jugal, partial left lacrimal and possible left quadratojugal. Kellner and Tomida (2000) regarded the diagnostic characters of this taxon as synapomorphies present in other pterosaur families, inconsequential, or dubious because of poor preservation of the holotype. Moreover, these authors argued that the CSRL 12692 / 12,713 did not share any autapomorphies of *Cearadactylus atrox*. Several pterosaur workers consider *Cearadactylus atrox* the only valid member of the genus *Cearadactylus* (Rodrigues and Kellner, 2013; Steel et al., 2005; Veldmeijer et al., 2005a; Vila Nova et al., 2014; Wang et al., 2009), with some noting that CSRL 12692 / 12,713 is potentially a chimera (Kellner and Tomida, 2000; Unwin, 2002; Veldmeijer et al., 2009; Vila Nova et al., 2014).

One of the more recently described species of pterosaur from the Romualdo Formation is *Unwindia trigonus* (SMNK PAL 6597), erected by Martill (2011) and on the basis of the anterior end of a partial premaxilla–maxilla. Martill (2011) originally regarded *Unwindia* as a ctenochasmatoid, based on comparisons with *Yixianopterus jingangshanensis* (Lü et al., 2006b) and the presence of relatively few teeth confined to the anterior end of the skull. *Unwindia* clearly differs from other pterodactyloids from the Santana Group, in that it has fewer teeth, with only seven tooth pairs present anterior to the anterior margin of the nasoantorbital fenestra, and less variation in tooth size (Martill, 2011). However, given that only four teeth are preserved in the holotype, the latter interpretation is largely based on the dimensions of the alveoli (Averianov, 2020; Martill, 2011). Based on the alveoli, the two anteriormost pairs of teeth were slightly larger in size (Martill, 2011). As noted by Martill (2011) the alveolar borders of *Unwindia* are raised, mirroring the condition observed in Lonchodectidae and other clades within Ornithocheiridae (e.g., Targaryendraconia and Tropeognathinae). More recently, Averianov (2020) regarded *Unwindia* as a taxon related to but outside of the Lonchodectidae, as it demonstrates greater variation in its dentition when compared with lonchodectids.

The first pterosaur material reported from the Araripe Basin was a partial right wing, designated the holotype specimen of '*Araripesaurus castilhoi*' (DGM 529-R; Price, 1971). The postcranial remains include a partial ulna and radius, carpals, pteroid, metacarpals and proximal end of the first wing phalanx, with no signs of distortion or crushing; and the ulna, radius and carpals still in articulation (Price, 1971). These elements were preserved in a limestone nodule, purportedly collected from the Pernambuco flank of the Chapada do Araripe (Price, 1971). Based on the preservation and association of elements present in the holotype specimen, Price (1971) surmised that more complete pterosaur skeletal remains could be found in the Araripe Basin. Unfortunately, the diagnosis of '*Araripesaurus castilhoi*' includes several characters that are more widespread within Ornithocheiroidea or more inclusive clades. This includes metacarpal III reaching the carpus, and reduction of metacarpals I and II (Price, 1971); similar configurations were observed in '*Santanadactylus pricei*' (Wellnhofer, 1991a). '*Araripesaurus castilhoi*' can be referred to the Ornithocheiridae, as the diameter of the radius is less than half that of the ulna (Price, 1971). Because of a lack of overlapping material, it remains uncertain as to whether any of the taxa based solely on cranial material can be ascribed to '*Araripesaurus castilhoi*'. This taxon was regarded as Pterodactyloidea *incertae sedis* by Barrett et al. (2008).

'*Araripedactylus dehmi*' (BSP 1975 I 166; Wellnhofer, 1977) was established on the basis of the proximal end of a first wing phalanx with fused extensor tendon process. Complete fusion between the two elements has obliterated any sutures, indicating the individual was osteologically mature (Wellnhofer, 1977). '*Araripedactylus dehmi*' does not possess any diagnostic features and has been regarded as Pterodactyloidea *incertae sedis* (Barrett et al., 2008).

In addition to the named taxa, various indeterminate ornithocheirid remains have also been reported from the Romualdo Formation. This includes the distal end of a three-dimensionally preserved ulna (DGEO-CTG-UFPE 7516) described by Aureliano et al. (2014) and tentatively referred to the Ornithocheiridae.

'*Santanadactylus brasilensis*' (sometimes misspelled '*Santandactylus*' or '*brasiliensis*') is a pterodactyloid established based on partial postcranial material that was briefly described by De Buisonjé (1980) and more fully described by De Buisonjé (1981). The holotype specimen comprises a right scapulocoracoid and humerus (UvA M 4894), whereas the putative paratype specimen comprises two articulated cervical vertebrae from the same locality (UvA M 4895). Bennett (1989) noted that the elongate cervical vertebrae with low neural spines present in UvA M 4895 were incongruent with those of other pteranodontoids, which are generally anteroposteriorly short, with tall neural spines. Although Kellner and Tomida (2000) noted that many of the proposed diagnostic characters of '*Santanadactylus brasilensis*' are more widespread within Pterodactyloidea, these authors regarded the presence of an almost straight ventral margin of the proximal and middle portions of the deltopectoral crest as a possible autapomorphy. Although other remains have been referred to '*Santanadactylus brasilensis*', specifically a scapulocoracoid (BSP 1987 I 65), Kellner and Tomida (2000) regarded this specimen as an indeterminate pterodactyloid. Similarly, the holotype material of '*Santanadactylus brasilensis*', '*Santanadactylus pricei*' and '*Santanadactylus spixi*' were considered non-diagnostic and excluded from the phylogenetic analysis of Andres et al. (2014). Moreover, the interpretation that the holotype and paratype are not conspecific (Bennett, 1989) seems likely, given that the paratype of '*Santanadactylus brasilensis*' is likely referable to *Tupuxuara longicristatus* (Averianov, 2014).

'*Santanadactylus pricei*' was erected by Wellnhofer (1985) based on BSP 1980 I 122, a partial left wing including ulna, radius, carpal elements, pteroid, metacarpals I-IV, a manual ungual claw and partial first wing phalanx. Referred specimens include an almost complete humerus (BSP 1980 I 43), partial wing comprising distal ends of the ulna and radius, fragmentary carpal element and proximal end of metacarpal IV (BSP 1980 I 120) and first and second wing phalanges (MZ A/III 522; Wellnhofer, 1985). BSP 1980 I 43 does not anatomically overlap with the holotype specimen, and its

referral to this taxon was based solely on size congruence (Wellnhofer, 1985). Wellnhofer and Kellner (1991) and Kellner and Tomida (2000) regarded '*Santanadactylus pricei*' as non-diagnostic, and designated the referred material previously allocated to this taxon as Pterodactyloidea indet. Similarly, Barrett et al. (2008) regarded '*Santanadactylus pricei*' as Pterodactyloidea *incertae sedis*.

'*Santanadactylus spixi*' (BSP 1980 I 121) was established based on a partial skeleton preserving elements from both the left and right wing (Wellnhofer, 1985). Although originally regarded as an ornithocheirid (Wellnhofer, 1985), based on the morphology of the carpal elements, Bennett (1989) referred '*Santanadactylus spixi*' to the Dsungaripteridae, a referral supported by Lü et al. (2009). By contrast, Kellner (1995) and Averianov et al. (2005) maintain that it is in fact a tapejarid. More recently, the taxon was regarded as a *nomen dubium*, likely referable to *Tupuxuara longicristatus* by Averianov (2014).

The first edentulous pterosaur taxon described from the Santana Group was *Tupuxuara longicristatus* (CD-R-003), established based on a partial skeleton (Kellner et al., 1988). The holotype specimen preserves a partial skull preserving the maxilla and high sagittal crest and part of the ring wing comprising metacarpals I-IV, the proximal end of the first wing phalanx; and part of the left wing comprising the distal end of metacarpal IV, proximal end of the first wing phalanx, and a manual ungual (Kellner et al., 1988). At the time of its initial description, *Tupuxuara longicristatus* was not allocated to a specific family (Kellner et al., 1988); however, it was subsequently assigned to Tapejaridae by Kellner (1989). It should be noted that the *Tupuxuara longicristatus* holotype does not preserve the anterior end of the skull, and is instead represented by the mid-section, preserving the anterior margin of the nasoantorbital fenestra (Kellner et al., 1988).

Tupuxuara leonardii (MCT 1495-R; Kellner et al., 1994) is represented by the anterior section of a partial skull including premaxilla, maxilla and palatines. Kellner et al. (1994) also referred a fragmentary skull (MN 6592-V), comprising partial rostrum and sagittal crest, to this taxon. Referral to the Tapejaridae is supported by the presence of a sagittal crest confined to the anterior section of the skull (Kellner et al., 1994). *Tupuxuara leonardii* differs from *Tupuxuara longicristatus* based on the presence of a strong, medial ridge on the palate that does not extend to the anterior portion of the skull (Kellner et al., 1994). Other cranial material referred to *Tupuxuara leonardii* includes a complete skull (IMCF 1052) and fragmentary yet almost complete skull of a reported juvenile (SMNK PAL 4330; Witton, 2009). Although Martill and Naish (2006) regarded *Tupuxuara leonardii* as a junior synonym of *Tupuxuara longicristatus*, on the basis that the palatal ridge varied because of individual variation in azhdarchoids, this claim was refuted by Kellner et al. (2007a).

The second edentulous pterosaur taxon described from the Santana Group was the tapejarid *Tapejara wellnhoferi*, which was established on the basis of a three-dimensionally preserved partial skull (MCT 1500-R/CD-R-080; Kellner, 1989). At the time of its initial description, the holotype specimen was housed in the Desiree Collection of Rainer Alexander von Blittersdorff (Kellner, 1989), but was subsequently acquired by and deposited in the Paleontology Section of the Departamento Nacional da Produgcio Mineral (Museu de Ciencias da Terra-DNPM) in Rio de Janeiro, Brazil (Kellner, 1996). The holotype preserves part of the premaxilla–maxilla, including an anterior sagittal crest, left lacrimal, jugal, quadratojugal and part of the quadrate (Kellner, 1989). In this regard, it anatomically overlaps with *Tupuxuara longicristatus* (Kellner et al., 1988; Kellner, 1989). Although it is difficult to constrain the ontogenetic status of the type specimen, Kellner (1989) indicated that the jugal, quadrate and quadratogjugal were firmly fused. The anterior tip of the premaxilla is missing. The relative positions of the nasoantorbital fenestra, orbit and lower temporal fenestra can be constrained based on the preserved part of the quadrate (Kellner, 1989). The species was diagnosed based on a combination of features, including large cranial crest near the anterior end of the skull, large nasoantorbital fenestra almost half the total length of the skull and ventrally deflected rostrum (Kellner, 1989). The presence of channels on the sagittal crest led Kellner (1989) to infer that these might be remnants of blood vessels, and that the crest might have performed a thermoregulatory function. In addition to the description of *Tapejara wellnhoferi*, Kellner (1989) erected the new clade Tapejaridae and allocated the two edentulous taxa *Tapejara* and *Tupuxuara longicristatus* to it. The cranial morphology of *Tapejara wellnhoferi* was later augmented with the description of two referred specimens (AMNH 2440 and SAO/UOSG 12891) by Wellnhofer and Kellner (1991). The more complete specimen, AMNH 2440, comprises an almost complete skull and two anterior cervical vertebrae, whereas SAO/UOSG 12,891 comprises the anterior end of the skull including the sagittal crest and the anterior margin of the nasoantorbital fenestra (Wellnhofer and Kellner, 1991). Despite missing the anterior ends of the premaxilla and mandibular symphysis, as well as the posterior end of the parietal, AMNH 2440 is exceptionally preserved, with the sclerotic ring preserved *in situ* within the orbit (Wellnhofer and Kellner, 1991). Based on the holotype and two referred specimens, Wellnhofer and Kellner (1991) figured a composite reconstruction of the skull of *Tapejara wellnhoferi*, concluding that the pointed and ventrally deflected tips of the jaws compared favourably with frugivorous extant birds. Although the jaws may have equally been well-adapted for scavenging carcasses, Wellnhofer and Kellner (1991) regarded this as unlikely, given that the preserved cervical vertebrae of AMNH 2440 were not elongated. Several workers regard tapejarids more generally as frugivores (see Pêgas et al., 2016); however, based on comparative anatomy and functional morphology, other diets have been proposed (see Bestwick et al., 2018b). As noted by Martill et al. (2020b), until preserved cololites / enterolites or irrefutable coprolites are discovered, the dietary preferences of this taxon and the Tapejaridae remains uncertain. At present, only one referred specimen of *Tapejara wellnhoferi* has been interpreted as a juvenile (SMNK PAL 1137; Eck et al., 2011). This specimen was later mentioned by Beccari et al. (2021), who compared the length of the appendicular elements and biometric ratios thereof of SMNK PAL 1137 with other tapejarids. Despite these comparisons, the specimen awaits formal description. The only specimen regarded as *Tapejara* cf. *T. wellnhoferi* comprises three cervical vertebrae (most likely IV–VI; AMNH 24445) that were described by Vila Nova et al. (2015). More recently, other pterosaur workers have more conservatively regarded the specimen as a tapejarine (Beccari et al., 2021; Buchmann et al., 2019; Leal et al., 2017). Another specimen referred to *Tapejara wellnhoferi* is IMNH 1053, which was figured but not described by Witton (2013), Pêgas et al. (2016) and Pêgas et al. (2018). IMNH 1053 was also mentioned by Veldmeijer et al. (2005a); however, those authors stated it was an ornithocheirid skull. More recently, the lengths of the appendicular elements of a specimen referred to *Tapejara wellnhoferi* (SMNK PAL 1157) were mentioned by Beccari et al. (2021). This partial postcranial skeleton awaits formal description.

Thalassodromeus sethi (DGM 1476-R; cast MN 6678-V) is represented by an incomplete skull and mandible with a large cranial crest (Kellner et al., 2002). The referral of *Thalassodromeus sethi* to Tapejaridae, proposed in the original description, is supported by the cranial crest and by the presence of a large nasoantorbital fenestra (Kellner et al., 2002). Although the cranial crest is incomplete posteriorly, it is well-preserved and possesses several branching channels along its lateral surface; these were interpreted by Kellner et al. (2002) as indicative of blood vessels.

Moreover, all elements are preserved three-dimensionally, with distortion limited to the right mandibular ramus and left jugal (Kellner et al., 2002). Kellner et al. (2002) suggested that *Thalassodromeus sethi* might have been a piscivorous skim-feeder, based on comparisons with modern skimmers (*Rynchops* spp.). However, experimental data indicates that such behaviour would not have been possible, owing to excessive drag (Bestwick et al., 2018b; Humphries et al., 2007).

Other material previously referred to *Thalassodromeus sethi* includes a partial edentulous mandibular symphysis (NMSG SAO 251093) derived from the Romualdo Member of the Santana Group (Veldmeijer et al., 2005b). At the time of publication, the specimen was held in a publically accessible yet private collection; however, the specimen has since been donated to the Naturmuseum St. Gallen, Switzerland (Headden and Campos, 2015). NMSG SAO 251093 is known from the anterior end of the mandibular symphysis, missing the anterior tip (Veldmeijer et al., 2005b). On both the left and right lateral surfaces, protuberances were observed; however, these are asymmetric, such that the right is larger when compared with the left (Veldmeijer et al., 2005b). Given that these are also associated with associated depressions on the surrounding cortical bone, Veldmeijer et al. (2005b) regarded these as the result of pathologies. Veldmeijer et al. (2005b) referred NMSG SAO 251093 to *Thalassodromeus sethi*, as both specimens possess a short, deep shelf posterior to the sharp-edged blade on the occlusal surface. However, they noted that the mandibular rami are more divergent in NMSG SAO 251093 when compared with the *Thalassodromeus sethi* type specimen (Veldmeijer et al., 2005b). More recently, Headden and Campos (2015) identified four apomorphic characters pertaining to NMSG SAO 251093 which were used to establish a new taxon, *Banguela oberlii*, which they referred to the Dsungaripteridae. Based on the phylogenetic analysis presented by Headden and Campos (2015), who modified the data matrix of Wang et al. (2010), *Banguela oberlii* was resolved as the successive sister taxon to *Dsungaripterus weii* + *Noripterus complicidens*. More recently, Pêgas et al. (2018), regarded the four autapomorphies proposed by Headden and Campos (2015) as all present in *Thalassodromeus sethi*, and thus insufficient to distinguish *Banguela oberlii* as a separate taxon. Pêgas et al. (2018) subsequently referred NMSG SAO 251093 to *Thalassodromeus sethi* and provided a revised diagnosis for this taxon. Despite these referrals, some workers maintain that *Banguela oberlii* is valid, with the taxon more recently regarded as a member of the Chaoyangopteridae by McPhee et al. (2020).

More recently, postcranial remains (AMNH 22567) were figured and described by Aires et al. (2014) who regarded the material as an indeterminate thalassodromid. AMNH 22567 preserves the final three cervical vertebrae, seven dorsal vertebrae (fused together to form the notarium), both scapulocoracoids, partial sternum, proximal end of the right humerus, partial wing phalanx and partial right hind limb. Aires et al. (2014) referred AMNH 22567 to the Thalassodromidae, based on the presence of foramina relative to the neural canal of the cervical vertebrae, and presence of a pneumatic foramen on the ventral side of the proximal end of the humerus.

Buchmann et al. (2017) described and figured a partial postcranial skeleton from the Romualdo Formation including three posterior cervical vertebrae (VII–IX), two partial scapulocoracoids and the proximal end of a right humerus (MN 6566-V). MN 6566-V was assigned to the Thalassodromidae on the basis of the morphology of the cervical vertebrae. Based on the fusion of the scapulocoracoids, MN 6566-V represents an osteologically mature individual (Buchmann et al., 2017).

'*Tupuxuara deliradamus*' (SMNK PAL 6410; Witton, 2009) was established based on a partial skull and was distinguished from *Tupuxuara leonardii* based on the morphology of the nasoantorbital fenestra and position of the orbit. Although Witton (2009) described a second specimen of '*Tupuxuara deliradamus*', neither the holotype nor the referred specimen anatomically overlaps with *Tupuxuara longicristatus*. '*Tupuxuara deliradamus*' was later considered a *nomen dubium* by Kellner (2013), who noted that the holotype is too incomplete (owing to erosion or preparation) to be taxonomically informative and that it can only be interpreted as an indeterminate azhdarchoid. Based on the figures presented by Witton (2009), it is clear that much of the frontal is represented by internal trabeculae, and the cortical bone of this element is no longer preserved. Moreover, Kellner (2013) regarded the referred specimen (KPMNH DL 84) as a composite, but indicated that the presence of a palatal ridge distinguishes it from *Caupedactylus ybaka*. More recently, Cerqueira et al. (2023) resolved '*Tupuxuara deliradamus*' within Tapejarinae and also regarded the taxon as a *nomen dubium*.

Indeterminate azhdarchoids from the Santana Group include a partial postcranial skeleton of a young juvenile (SMNK PAL 3985; Elgin and Hone, 2013) and a fragmentary palate comprising maxilla, vomers and possible palatines (MPSC R 859; Pinheiro and Schultz, 2012). SMNK PAL 3985 preserves at least five cervical and six thoracic vertebrae; sternal plate and pectoral girdles, elements from both the left and right wing, and the left femur (Elgin and Hone, 2013). The ontogenetic status of SMNK PAL 3985 is indicated by several unfused elements, including but not limited to the dorsal neural arches that are fossilised separately from their respective centra, scapula and coracoid (fused together as the scapulocoracoid in osteologically mature individuals), carpals, and unfused elements in the pelvis (Elgin and Hone, 2013). Although they did not speculate on the taxonomic position of this specimen, Elgin and Hone (2013) analysed the internal pneumaticity of several elements present in SMNK PAL 3985. Buchmann et al. (2021) further described the internal pneumaticity of the cervical vertebrae in SMNK PAL 3985.

Comparisons of MPSC R 859 with other pterosaurs from the Santana Group are somewhat limited, as this portion of the skull is rarely fossilised and can only be accurately assessed in three-dimensionally preserved specimens. Although Pinheiro and Schultz (2012) noted that the palate of MPSC R 859 differed from the condition of all other pterosaurs from which a palate is known and that it likely represented a new taxon from this stratigraphic horizon, they did not erect a new species.

3.3.12. Lohan Cura Formation, Argentina

The earliest report of pterosaur material from the Lohan Cura Formation (Neuquén Province, Argentina) was of isolated teeth (MCF-PVPH-741 and MCF-PVPH-743) from the Albian, figured and described by Martinelli et al. (2007). The teeth were referred to the Pterosauria because of their similarity to teeth assigned to ornithocheirids from South America (Martinelli et al., 2007). Given the teeth are labiolingually compressed and anteroposteriorly curved, assignment to the Pterosauria cf. Ornithocheiridae is supported here. The only other pterosaur material reported from the Lohan Cura Formation is an incomplete but three-dimensionally preserved ulna (MCF-PVPH-881) from the Cerro de los Leones locality, comprising the proximal articular surface and part of the diaphysis. Although more precise taxonomic referral was not possible, Bellardini (2016) regarded MCF-PVPH-881 as a medium-sized pterodactyloid, and a probable ornithocheirid. Histological analysis of MCF-PVPH-881 indicates the primary cortical outer layer differs in terms of its organisation when compared with other pterosaurs (Bellardini, 2016; Bellardini and Codorniú, 2019). As noted by Bellardini (2016), MCF-PVPH-881 lacks both the circumferentially oriented lamellae (OCL) present in *Rhamphorhynchus* (MTM V 2008.33.1; Prondvai et al., 2012) and the "plywood" struc-

ture of *Montanazhdarcho* (De Ricqlès et al., 2000) and the ornithocheirid UOP 2000.3 (Steel, 2003, 2008).

3.3.13. Goio-Erê Formation, Brazil

Two edentulous pterosaur taxa have been reported from the Aptian–Albian Goio-Erê Formation. The first taxon described from this horizon is the tapejarid *Caiuajara dobruskii*, reported by Manzig et al. (2014) and based on multiple individuals. At the time of its initial description, the holotype specimen was reported from a monotypic bone bed with at least 47 others, varying in ontogenetic stage (Manzig et al., 2014). The discovery of tens of individuals varying in age was interpreted by Manzig et al. (2014) as evidence of gregariousness supporting the notion that members of this taxon lived in colonies. Other pterosaur colonies have been reported from the Loma del *Pterodaustro* from the Lagarcito Formation (Chiappe et al., 1998a; Grellet-Tinner et al., 2014) and hundreds of pterosaur bones reported by Bell and Padian (1995) from the Atacama Region (Quebrada Monardes Formation). The holotype specimen of *Caiuajara* (CP.V 1449) is a partial skeleton, interpreted as an adult, that preserves a partial skull and lower jaw, cervical vertebrae and appendicular elements. An additional twenty paratypes of *Caiuajara* are deposited in the same collection (Supplementary Material 1), with the taxon also known from several referred specimens (Manzig et al., 2014). Despite variation in the wingspans of individuals from this bone bed (0.65–2.35 m), the authors observed little to no ontogenetic variation in the appendicular elements; by contrast, the angle of the premaxillary crest became progressively steeper through ontogeny, with the crest inclined at approximately 90° in adults (Manzig et al., 2014). Based on the phylogenetic analysis presented by Manzig et al. (2014), *Caiuajara* was placed in a polytomy with *Tupandactylus*, *Europejara*, *Tapejara*, *Sinopterus* and *Eopteranodon*.

More recently, Kellner et al. (2019c) described a second taxon from the Goio-Erê Formation: *Keresdrakon vilsoni*, which which originally was regarded as a tapejaromorph but has more recently been resolved within Tapejaridae (Andres, 2021). The holotype of *Keresdrakon* is a partial skeleton (CP.V 2069), known from a partial skull, cervical and dorsal vertebrae, fragmentary gastralia, sternum, appendicular elements, part of the pelvis, partial hind limb and associated fragments (Kellner et al., 2019c). Similar to *Caiuajara*, *Keresdrakon* is also known from multiple individuals (Supplementary Material 1). Interestingly, *Keresdrakon* and *Caiuajara* were found at the same locality (referred to as the 'Cemitério dos Pterossauros' site), indicating sympatry between the two edentulous taxa (Kellner et al., 2019c). Although this is far from being the first instance in which more than one pterosaur taxon has been identified from the same stratigraphic horizon, Kellner et al. (2019c) argue that the preservation of this material in a bone bed offers direct evidence that the two taxa shared the same environment. Based on the pterosaur assemblage at this site, remains ascribed to *Caiuajara* were much more common when compared with *Keresdrakon*, with more than 100 individuals referred to *Caiuajara* (Kellner et al., 2019c). By contrast, Kellner et al. (2019c) noted the presence of at least three individuals of *Keresdrakon*; however, other isolated material was also referred to this taxon. *Keresdrakon* differs from *Caiuajara* in that a sagittal crest is not apparent until the anterior margin of the nasoantorbital fenestra in the former (Kellner et al., 2019c), whereas in *Caiuajara* both juveniles and adults possess anteriorly positioned premaxillary crests (Manzig et al., 2014). Differentiating between the two based on appendicular elements is more difficult; however, subtle yet salient differences were observed in the pneumatic foramina (Kellner et al., 2019c). The laterally positioned pneumatic foramina present on each side of the middle cervical vertebrae of *Keresdrakon* are larger when compared with those of *Caiuajara*, and *Keresdrakon* possesses an additional pneumatic foramen on the proximal end of the first wing phalanx (Kellner et al., 2019c). Moreover, *Caiuajara* bears a pneumatic foramen on the dorsal surface of the proximal end of the humerus, which is absent in *Keresdrakon* (Kellner et al., 2019c). The occurrence of these edentulous taxa, represented by juveniles and adults, combined with their depositional environment was interpreted by both Manzig et al. (2014) and Kellner et al. (2019c) as mortality events near an oasis. Although multiple individuals of both taxa are preserved at this site, the remains of *Caiuajara* and *Keresdrakon* are disarticulated, with partial skeletons attributed to a single individual vanishingly rare (Kellner et al., 2019c). This suggests their carcasses were exposed for some time, rather than buried quickly, and were subsequently fossilised together during high energy, aeolian events (Kellner et al., 2019c).

3.3.14. Lagarcito Formation, Argentina

The Loma del *Pterodaustro* locality (Albian Lagarcito Formation) has famously yielded numerous specimens of the filter-feeding *Pterodaustro guinazui* (Bonaparte, 1970; Casamiquela and Diaz, 1980; Chiappe et al., 2000; Chiappe and Chinsamy, 1996; Sanchez, 1973). Codorniú and Gasparini (2007) noted that over 250 specimens had been prepared, and many others had been collected but awaiting preparation. The holotype specimen of *Pterodaustro* (PVL 2571) is an almost complete right humerus, missing the epicondyle (Bonaparte, 1970). Referred specimens described with the holotype include a partial femur missing the femoral head (PVL 2572), partial first wing phalanx (PVL 2573), a complete cervical vertebra (PVL 2574), scapulocoracoid missing part of the scapula (PVL 2585), an incomplete skull fragment (PVL 2586), the proximal end of a tibia-fibula (PVL 3403) and two dorsal vertebrae (PVL 2575); all of these specimens were collected from the same locality (Bonaparte, 1970). *Pterodaustro* was referred to the Pterodactyloidea by Bonaparte (1970), based on the morphology of the appendicular elements. *Pterodaustro* differs from other pterosaurs in that the premaxilla–maxilla and mandible are bowed, such that the mid-section of the skull is the ventrally lowest point (Bonaparte, 1971; Chiappe and Chinsamy, 1996; Sanchez, 1973). Longitudinal and transverse sections through the middle section of the mandible confirms the presence of thin, densely packed, needle-like teeth, each with slender conical bases and spatulate crowns (Chiappe and Chinsamy, 1996). Unlike the dentition of other pterodactyloids, each individual likely bore hundreds of teeth (Chiappe and Chinsamy, 1996). Moreover, the teeth of *Pterodaustro* were not confined within alveoli, but likely embedded in keratin (Chiappe and Chinsamy, 1996). Previously it was assumed that *Pterodaustro* did not possesses true teeth (Wellnhofer, 1991b); however, the mandible and dentition therein did likely function similar to baleen, meaning that this taxon was primarily filter feeding (see Bestwick et al., 2018b). As noted by Codorniú and Gasparini (2007), only two complete and articulated specimens of *Pterodaustro* have been reported (PVL 3860 and MMP 1089); however, four articulated postcranial skeletons are also known. The discovery of specimens of *Pterodaustro* with *in situ* teeth not only shed light on the novel dentition of this taxon, but more importantly permitted other workers to reassess the phylogenetic position of this once enigmatic pterosaur. Phylogenetic analyses conducted by Unwin (1995) and Kellner (2001a) recovered *Pterodaustro* within Ctenochasmatoidea, a referral which has not been disputed since. The occurrence of poorly-sorted coarse sand to fine gravel in the thoracic section of two near-complete adult individuals (MIC-V263 and MIC-V243), was interpreted by Codorniú et al. (2013) as evidence for gastroliths in this pterosaur. This interpretation is supported by the localities from which these specimens were collected, which consist of medium siltstone and claystone, with very fine sand (Codorniú et al., 2013). Although gastroliths have been reported in other archosaurs and modern birds, *Pterodaustro* is the first pterosaur with stomach stones and these were

likely ingested to aid in the mechanical digestion of hard food items, including "shelled crustaceans" (Codorniú et al., 2013). Also reported from the Loma del *Pterodaustro* are juveniles of *Pterodaustro* (MHIN-UNSL-GEO-V 241; Codorniú and Chiappe, 2004b) and an unhatched egg with embryo (MHIN-UNSL-GEO-V 246; Chiappe et al., 2004); these have enabled ontogenetic analyses to be undertaken (Chinsamy et al., 2008; Chinsamy et al., 2009). Based on the proportions of two juveniles (MHIN-UNSL-GEO-V 241 and MMP 1168) when compared with adult individuals, Codorniú and Chiappe (2004a) noted at least five significant allometric transformations in *Pterodaustro*. More recently, a partial egg assigned to *Pterodaustro* (MIC-V 778; Grellet-Tinner et al., 2014), has been reported also from the same locality and is preserved in three-dimensions. Based on differences in the composition of MIC-V 778, as compared with those of related taxa from China, Grellet-Tinner et al. (2014) concluded that these nesting conditions were analogous to those of grebes or flamingos occupying similar settings.

3.3.15. Chulec Formation, Peru

An almost complete pteranodontid humerus (BHI 1276), most likely derived from the Albian Chulec Formation, constitutes the only known pterosaur material from Peru (Bennett, 1989). The pteranodontid affinities of this specimen have been questioned by Averianov and Arkhangelsky (2020). We follow Averianov and Arkhangelsky (2020) and regard BHI 1276 as Pterosauria indet.

3.3.16. Exu Formation, Brazil

To date, the only pterosaur material reported from the upper Albian–lower Cenomanian Exu Formation (Piaui, Brazil) is an incomplete but three-dimensionally preserved humerus (SMNK PAL 6414), described by Martill (2008). Although SMNK 6414 comprises part of the proximal end of a humerus, it does not preserve the proximal articular surface and is poorly preserved, such that the cortical bone has been eroded, with the internal trabeculae infilled with ironstone (Martill, 2008). Martill (2008) noted that the proximal expansion of the diaphysis of SMNK PAL 6414 resembles the condition of *Tapejara* and *Lonchodectes*.

3.3.17. Alcântara Formation, Brazil

The only pterosaur material reported to date from the Cenomanian Alcântara Formation are isolated teeth from the Laje do Coringa (Alcântara Municipality, Maranhão, Brazil), which were figured and described by Elias et al. (2007). The nine teeth (URC R.77–1 – URC R.77–5, UFMA 1.20.178–1, UFMA 1.20.166, UFMA 1.20.130 and UFMA 1.20.1744) are well-preserved, with at least four morphotypes present; morphotypes 1 and 2 were regarded as indeterminate ornithocheirids, whereas morphotypes 3 and 4 were referred to the more inclusive Ornithocheiroidea (Elias et al., 2007).

3.3.18. Candeleros Formation, Argentina

The Cenomanian Candeleros Formation of the Rio Limay Subgroup has yielded pterosaur tracks, including manus-pes sets assigned to the ichnotaxon Pteraichnidae (Calvo and Lockley, 2001). The sites, located near Lake Ezequiel Ramos Mexía in Neuquén Province, preserve the first reported pterosaur trackways from Gondwana (Calvo and Lockley, 2001). A partial pterosaur wing comprising ulna, radius, articulated syncarpals, metacarpal IV and the proximal end of the first wing phalanx (MPCN 102), as well as a partial ulna (MPCN 101), have also been reported from the Candeleros Formation (Apesteguía et al., 2007; Haluza et al., 2007). MPCN 101 was originally assigned to the Tapejaroidea, whereas the partial wing (MPCN 102) was interpreted as a basal pterosaur; however, Codorniú and Gianechini (2016) have questioned the taxonomic affinities of both specimens. An incomplete ulna (MMCh-PV 53) attributed to a pterosaur with a wingspan of 1.5 m has also been reported from the Candeleros Formation (Haluza and Canale, 2009). Codorniú and Gianechini (2016) suggested this ulna belongs to an indeterminate pterodactyloid.

3.3.19. Bajo Barreal Formation, Argentina

At present, pterosaur remains from the lower Cenomanian–upper Turonian Bajo Barreal Formation (Central Patagonia, Argentina) are solely represented by a three-dimensionally preserved first wing phalanx, missing the distal end (UNPSJB-Pv 1009; Ibiricu et al., 2012; Ibiricu et al., 2019). Based on the fusion of the extensor tendon process, with no discernible suture, Ibiricu et al. (2012) regarded UNPSJB-Pv 1009 as an adult or osteologically mature individual. Although UNPSJB-Pv 1009 was interpreted as an indeterminate pterosaur (Ibiricu et al., 2012), it can likely be referred to Pterodactyloidea based on its stratigraphic age.

3.3.20. Portezuelo Formation, Argentina

The upper Turonian–lower Coniacian Portezuelo Formation in Neuquén Province has yielded isolated pterosaur remains. An incomplete ulna (MUCPv-358), which was the first pterosaur reported from this unit, was attributed to an osteologically immature individual with an estimated wingspan of 6 m (Kellner et al., 2004). Codorniú and Gasparini (2007) subsequently regarded MUCPv-358 as an indeterminate azhdarchid, based on the morphology of the proximal epiphysis. Additional remains from the Portezuelo Formation include a partial ulna and radius (both MUCPv-600) and the proximal end of a first wing phalanx lacking the extensor tendon process (MUCPv-359; Kellner et al., 2006). Kellner et al. (2006) referred MUCPv-600 and MUCPv-359 to the Pterodactyloidea.

An incomplete edentulous jaw (MUCPv-1137) from the Portezuelo Formation near Neuquén City in Argentina was used to establish the taxon *Argentinadraco barrealensis* (Kellner and Calvo, 2017). *Argentinadraco* can be distinguished from other azhdarchoids as it bears a small dentary sagittal crest, and lacks a ventral sulcus (Kellner and Calvo, 2017).

3.3.21. Plottier Formation, Argentina

A large pterosaur humerus (UNCUYO-LD 350) from the upper Coniacian–lower Santonian Plottier Formation in the northern Neuquén Basin, Argentina constitutes one of the largest South American pterosaurs, with an estimated wingspan of 9.1 m (Ortiz et al., 2017). UNCUYO-LD 350 was noted as possessing characters of both the Tapejaridae as well as the Azhdarchidae. UNCUYO-LD 350 was found in association with the postcranial remains of a smaller individual comprising thirty bones (UNCUYO-LD 307; Ortiz et al., 2017). The latter (UNCUYO-LD 307) was recently designated the holotype specimen of the newly erected taxon, *Thanatosdrakon amaru*, with UNCUYO-LD 350 the paratype (Ortiz David et al., 2022). Both these specimens are three-dimensionally preserved, with UNCUYO-LD 307 comprising a partial skeleton represented by axial, appendicular and pelvic elements; complete fusion of the notarium and scapulocoracoid indicate that this individual was osteologically mature (Ortiz David et al., 2022). Based on comparisons with the medium-sized azhdarchid *Zheijangopterus* (ZMNH M1323; Cai and Wei, 1993; Unwin and Lü, 1997), UNCUYO-LD 307 has an estimated wingspan of $\sim$ 7 m. Phylogenetic analysis resolves *Thanatosdrakon* as an azhdarchid, sister to *Quetzalcoatlus northropi* and *Quetzalcoatlus lawsoni* (Ortiz David et al., 2022).

3.3.22. Bajo de la Carpa Formation, Argentina

The only pterosaur material reported from the Santonian Bajo de la Carpa Formation is a first wing phalanx of a large-bodied individual (MPCN-PV 103), mentioned but not described by Apesteguía

et al. (2007), and collected from the La Bonita locality (Río Negro, Argentina). It was not stated whether the specimen preserved the proximal articular surface and whether or not this specimen preserves an extensor tendon process. Although Apesteguía et al. (2007) also mentioned a tapejaroid from the Candeleros Formation, the pterosaurian affinities of this specimen has since been questioned by Codorniú and Gianechini (2016). When summarising the vertebrate assemblage of the Bajo de la Carpa Formation, Cruzado-Caballero et al. (2016) noted the only pterosaur material from this stratigraphic horizon was an "unnamed azhdarchid" (p. 53). However, although Apesteguía et al. (2007) noted that the size of this element was concordant with azhdarchids from the Late Cretaceous, they did not explicitly refer MPCN-PV 103 to that clade. As such, MPCN-PV 103 is regarded here as Pterosauria indet.

3.3.23. Anacleto Formation, Argentina

At present, the only pterosaur remains reported from the Campanian Anacleto Formation are four pterosaur manus tracks, reported from fluvial red beds in the Río Negro Province, northern Patagonia (Díaz-Martínez et al., 2022). The identification of pterosaurian pes tracks will elucidate the taxonomic affinities of the Anacleto Formation ichnotaxa.

3.3.24. Allen Formation, Argentina

Aerotitan sudamericanus was established on the basis of a partial rostrum (MPCN-PV 0054), derived from the middle Campanian–lower Maastrichtian Allen Formation in Río Negro Province, Argentina and was referred to the Azhdarchidae (Novas et al., 2012). Kellner and Calvo (2017) have suggested MPCN-PV 0054 may in fact be a dentary, noting that it appears more slender when compared with *Argentinadraco*.

3.3.25. Uncertain stratum, Brazil

A partial left humerus (DGM 238-R) from a Maastrichtian-age limestone in Brazil forms the basis for '*Nyctosaurus*' *lamegoi* (Price, 1953). This is the geologically youngest Cretaceous pterosaur known from South America, and, if correctly identified, one of the few Gondwanan nyctosaurids.

4. Africa

4.1. Jurassic pterosaurs of Africa

4.1.1. Upper Elliot Formation, South Africa

Indeterminate pterosaur remains were reported by Blackbeard and Yates (2007) from the Hettangian–Sinemurian Upper Elliot Formation (Yates et al., 2004). Specifically, the aforementioned remains comprise the shafts of two appendicular elements with thin cortical bone (see Yates et al., 2010: supplementary material). This material awaits formal description.

4.1.2. Clarens Formation, South Africa

Several ichnotaxa have been reported from the Clarens Formation (van Dijk, 1978; Van Dijk, 2001; van Dijk and Eriksson, 2021), which is regarded as Sinemurian–Pliensbachian in age (Bordy et al., 2020). Although the majority of these tracks have been attributed to small, bipedal dinosaurs, the identity of the *Saltirecarpipes tinleyi* ichnotaxon might have been pterosaurian (van Dijk and Eriksson, 2021). The identification of consecutive trackways will undoubtedly shed further light on the diversity of the Lower Clarens Formation.

4.1.3. Anoual Formation, Morocco

Isolated pterosaur teeth have been reported from the Bathonian Anoual Formation, with material collected from three different sites across Guelb El Ahmar (Anoual Syncline; Haddoumi et al., 2016). Two different morphotypes have been identified: one characterised by slender, labiolingually compressed crowns with sharp anterior and posterior carinae, regarded as an indeterminate rhamphorhynchid (GEA 2–7; Haddoumi et al., 2016); and another characterised by being more robust and shorter apicobasally, with some evidence of vertical folds developed along the lingual surface near the base in areas preserving enamel (GEA 2–6, GEA 2–50, GEA 2–51; Haddoumi et al., 2016). Haddoumi et al. (2016) noted that similar teeth are present in *Darwinopterus robustodens* as well as some Middle Jurassic rhamphorhynchids. Although the authors regarded the latter as those from indeterminate pterodactyloids, Haddoumi et al. (2016) noted that this morphotype is more characteristic of Middle Jurassic pterosaurs from Laurasia and differs from penecontemporaneous remains from Gondwana.

4.1.4. Tendaguru Formation, Tanzania

Pterosaur remains from the Upper Jurassic (Kimmeridgian–Tithonian) Tendaguru Formation of Africa were first mentioned by Janensch (1914), who surmised that at least two different taxa were present, based on an apparent size discrepancy (Unwin and Heinrich, 1999). Although pterosaurs were also noted by Parkinson (1930), the first description of pterosaur remains from Africa was published by Reck (1931), who described material collected during expeditions from 1909 to 1913 that was subsequently deposited in the Museum für Naturkunde of the Humboldt University in Berlin. Reck (1931) erected four new species of pterosaur from Tendaguru: '*Rhamphorhynchus tendagurensis*', '*Pterodactylus maximus*', '*Pterodactylus brancai*', and '*Pterodactylus arningi*', all four of which were established on the basis of isolated fore- and hind limb elements. Additional material referred to '*Pterodactylus brancai*' includes three tibiotarsi (HMN Nr. 2; HMN Nr. 6; NHMUK PV R9191), ascribed to the Upper Jurassic Tendaguru Formation of Africa (Galton, 1980). As noted by Wellnhofer (1978), fore- and hind limb elements rarely possess characters diagnostic at even low taxonomic levels. Unwin and Heinrich (1999) considered the four taxa erected by Reck (1931) as *nomina dubia*, concluding that although some remains might represent rhamphorhynchids, further study is required before their identity can be established more precisely.

Presently, a single valid pterosaur taxon is recognised from Tanzania: the *Tendaguripterus recki* (MB.R.1290; Unwin and Heinrich, 1999) from the Upper Jurassic Tendaguru Formation (Kellner et al., 2007a). The holotype specimen is known from a posterior portion of a fused mandibular symphysis bearing teeth and was considered by Unwin and Heinrich (1999) as a dsungaripteroid (sensu Unwin, 2003). Despite extensive excavation of the Tendaguru Formation, resulting in the collection of more than 200 pterosaur specimens (Unwin and Heinrich, 1999), the majority of the remains are fragmentary and comprise bone shafts lacking articular ends (Unwin and Heinrich, 1999).

Elongate cervical vertebrae have also been reported from the Tendaguru Formation (Costa et al., 2015; Sayão and Kellner, 2001a, b). In their original description, Sayão and Kellner (2001a) interpreted MB.R.2832 as a cervical vertebra from an indeterminate azhdarchid. The azhdarchid affinities of MB.R.2832 were later questioned by Andres and Qiang (2008), who referred it to the Ctenochasmatidae on the basis of lateral foramina. More recently, the presence of lateral foramina was disputed by Costa et al. (2015), who tentatively suggested MB.R.2832, as well as an additional cervical vertebra, MB.R.2823, pertain to azhdarchid pterosaurs. If MB.R. 2832 is in fact an azhdarchid, it would extend the temporal range of the clade to the Kimmeridgian–Tithonian (Costa et al., 2015). Given that no other azhdarchids are known from the Late Jurassic (Averianov, 2014), additional material will be needed to ascertain whether azhdarchids were present during

this period. Costa et al. (2015) also figured and described other isolated pterosaur elements from the Tendaguru Formation, including a wing metacarpal, MB.R. 2821 (cast MN 6651-V), ascribed to the Azhdarchoidea, and a coracoid, MB.R.2830 (cast MN 6663-V), interpreted as a new basal pterodactyloid. MB.R.2830 is unusual in that it bears three well-developed pneumatic foramina, as well as a lateral depression on the posterior face of the acrocoracoid process, a feature not known in any other pterosaur (Costa et al., 2015).

Two incomplete pterosaur humeri have also been reported from the Tendaguru Formation: 1) MB.R.2828 (cast MN 6661-V) and 2) MB.R.2833 (cast MN 6666-V) (Costa and Kellner, 2009). MB.R.2828 was interpreted as a new dsungaripteroid taxon, on the basis of its unique deltopectoral crest morphology, which differs from the hatchet-shaped crest observed in the Rhamphorhynchidae and subrectangular condition of the Campylognathoididae (Costa and Kellner, 2009). The other partial humerus, MB.R.2833, was identified as an indeterminate archaeopterodactyloid of small size, with a suggested wingspan of only 35 cm (Costa and Kellner, 2009). For more precise information regarding the stratigraphic position of pterosaur remains from the Tendaguru Formation, see Kellner et al. (2007a) tab. 1.

4.2. Cretaceous pterosaurs of Africa

4.2.1. Upper Lualaba Series, Congo

The earliest report of Cretaceous pterosaur remains from Africa is the distal end of a left metacarpal (lacking specimen number; Swinton, 1948) from Lower Cretaceous sediments of the upper Lualaba Series along the Lubilash River, Democratic Republic of Congo (Cahen, 1954; Roberts et al., 2015). Although this specimen was originally assigned to cf. *Ornithocheirus* by Swinton (1948), more recently, Kellner et al. (2007a) suggested that it is better to regard this specimen as Pterodactyloidea indet. in light of its incompleteness and Cretaceous age.

4.2.2. High atlas Mountains, Morocco

The geologically oldest Cretaceous pterosaur remains from Africa are isolated teeth, mentioned but not described by Sigogneau-Russell et al. (1998). The teeth (provisional specimen numbers SA 100–104) were recovered from a Berriasian-aged calcareous lens within the High Atlas Mountains near Talsinnt (Knoll, 2000). These were regarded by Knoll (2000) as ornithocheirid or possibly gnathosaurines. Rodrigues and Kellner (2010) questioned the taxonomic affinities of 'gnathosaurine' teeth, noting that they might also represent ornithocheirids.

4.2.3. Douiret Formation, Tunisia

Isolated pterosaur teeth from the lower Aptian Douiret Formation were alluded to by Fanti et al. (2016), with other vertebrates including elasmobranchs, actinopterygians, dipnoans and the teleosaurid *Machimosaurus rex*. These pterosaur teeth await formal description.

4.2.4. Elrhaz Formation, Niger

From the Aptian–Albian Elrhaz Formation of Niger only isolated pterosaur remains have been identified, including a near-complete left humerus referred to the Tapejaridae and incomplete right wing referred to the Ornithocheiridae. The referral of these remains (both lacking specimen numbers) was based on the morphology of the carpus and reduction in metacarpals II and III (Blackburn, 2002). More recently, a labiolingually recurved tooth (MNN GAD16) with striations along its base was figured by Sereno and Brusatte (2008) and regarded as an ornithocheirid.

4.2.5. Chenini Formation, Tunisia

The lower Albian Chenini Formation in the Tataouine region of southern Tunisia has produced an ornithocheirid tooth (lacking specimen number; Benton et al., 2000).

4.2.6. Aïn el Guettar Formation, Tunisia

The second pterosaur tooth reported from Tunisia was embedded in matrix (RH45 – 1a), from the Albian Oum ed Diab Member of the Aïn el Guettar Formation (Martill et al., 2018a). This tooth is slightly recurved, with bifurcating ridges and was regarded by Martill et al. (2018a) as an ornithocheirid, based on comparisons with *Ludodactylus sibbicki* and '*Tropeognathus robustus*' which preserve *in situ* teeth with similar ornamentation.

4.2.7. Gara Samani Formation, Algeria

At present, the only pterosaur material reported from the uppermost Albian–lower Cenomanian Gara Samani Formation of southern Algeria are two isolated teeth (LGS-37 and LGS-38) from the Samani Vertebrate-rich Sand Member (Benyoucef et al., 2022). These teeth bear striations and were regarded as Ornithocheiridae indet. (Benyoucef et al., 2022).

4.2.8. Kem Kem Group, Morocco

The pterosaur record of the Kem Kem Group of Morocco is diverse, although most pterosaur remains described from this unit are fragmentary despite being three-dimensionally preserved. The Kem Kem Group pterosaur assemblage has recently been summarised in detail by Smith et al. (2022); although aspects of that paper will be mentioned here, we direct the reader to this comprehensive review paper. To date, the assemblage has been reported to include ornithocheirids (Jacobs et al., 2019; Jacobs et al., 2020; Mader and Kellner, 1999; Wellnhofer and Buffetaut, 1999a), indeterminate azhdarchoids (Martill et al., 2018b; Smith et al., 2020; Smith et al., 2022) tapejarids (Martill et al., 2020b; Wellnhofer and Buffetaut, 1999b), chaoyangopterids (McPhee et al., 2020), and azhdarchids (Kellner and Mader, 1996; Labita and Martill, 2021; Martill et al., 2018b). Although a partial edentulous mandibular symphysis (MN 7054-V) was originally regarded as a pteranodontid by Kellner et al. (2007a), it was later interpreted as a tapejarid by Ibrahim et al. (2020), and more recently a referred specimen of *Afrotapejara zouhrii* by Smith et al. (2022). The Kem Kem Group comprises the Ifezouane and Aoufous formations, and has been interpreted to represent a fluvial to deltaic setting (Belvedere et al., 2013; Martill and Ibrahim, 2015; Wellnhofer and Buffetaut, 1999a). For more precise information regarding the stratigraphy see Ibrahim et al. (2020), and Rodrigues et al. (2011) and references therein. As noted by Martin et al. (2016) the Kem Kem Group is most likely late Albian to early Cenomanian in age.

To date, ornithocheiroids are known from the Kem Kem Group of Morocco based on isolated cranial remains, a notarium and isolated teeth (see Smith et al., 2022 and references therein). The first ornithocheiroid and pterosaur taxon described from the Kem Kem Group was *Siroccopteryx moroccensis* (LINHM 016), recovered from red beds (Ifezouane Formation) of Hamada du Guir near Taouz (Mader and Kellner, 1999). The holotype and only known specimen comprises a fragmentary upper jaw preserving partial premaxillary crest and *in situ* teeth (Mader and Kellner, 1999). As noted by Smith et al. (2022), the present location of the holotype specimen, LINHM 016 is not known. Mader and Kellner (1999) regarded *Siroccopteryx* as an ornithocheirid, based on the dorsal margin of the premaxilla narrowing posteriorly, which they interpreted as remnants of a premaxillary crest, which at the time was considered synapomorphic of the Ornithocheiridae. However, the taxonomic affinities of *Siroccopteryx* were later questioned by Unwin (2001) who noted LINHM 016 is near identical to *Uktenadactylus wadleighi* and

regarded it as a junior synonym of *Coloborhynchus*. Despite these comparisons, *Siroccopteryx moroccensis* has been maintained as a valid taxon by other pterosaur workers (Andres, 2021; Bantim et al., 2014; Martill et al., 2018b; Rodrigues and Kellner, 2008). The external surface of *Siroccopteryx* is marked by rugosities, shallow pits and meandering striations, with some features superficially resembling those of cranial sutures (Mader and Kellner, 1999). Given that the position of these grooves does not correspond to those of actual cranial sutures, Mader and Kellner (1999) suggested these may be pathological features. This interpretation is supported by an anomalous growth near the fourth and fifth tooth positions on the left, which was interpreted as a vestigial abscess (Mader and Kellner, 1999). As noted by Mader and Kellner (1999), *Siroccopteryx* differs from *Anhanguera* in that the largest tooth of the premaxilla–maxilla in the former is the 3rd tooth position. In this regard, *Siroccopteryx* is more similar to *Ferrodraco*, with the third tooth pair larger than the fourth in both the upper and lower jaws, based on their alveolar diameters (Pentland et al., 2022a). More recent phylogenetic analyses have resolved *Siroccopteryx* as the sister taxon to *Tropeognathus mesembrinus* with *Mythunga camara* + *Ferrodraco lentoni* as the successive sister taxon to this clade (Holgado and Pêgas, 2020; Pentland et al., 2022a). Alternatively, *Siroccopteryx* is resolved as the sister taxon to *Ornithocheirus simus*, with *Tropeognathus* as the successive sister taxon to this clade (Jacobs et al., 2019).

An isolated tooth (LINHM 007) from an Albian/Cenomanian unit near Hamada du Guir, Taouz in the Errachidia Province (formerly Ksar Es Souk Province) was tentatively interpreted as pterosaurian (Kellner and Mader, 1997). Such an interpretation seems likely, given the tooth morphology is congruent with the Ornithocheiridae, combined with the occurrence of the ornithocheirid *Siroccopteryx moroccensis* from the same area.

The oxygen and carbon isotope composition of isolated ornithocheirid teeth recovered from the Bou Laalou, Chaaft, Takemout, Jebel Al Qabla and Zaouia localities across the Ifezouane Formation of the Kem Kem Group of Morocco were analysed by Amiot et al. (2010). The $\delta^{18}O_P$ values of the ornithocheirid pterosaur teeth were within the range of other terrestrial animals, whereas the low and restricted $\delta^{13}C_c$ values indicate a diet largely comprising freshwater rather than marine material (Amiot et al., 2010).

More recently, Smith et al. (2022) regarded 44 isolated teeth as indeterminate ornithocheirids, noting that the abundance of these remains suggests this clade was an important component of this assemblage. For specific specimen numbers, see Supplementary Material 1.

The second ornithocheirid taxon described from the Kem Kem Group (Ifezouane Formation) of Morocco is *Coloborhynchus fluviferox*, established based on a fragmentary maxilla (FSAC-KK 10701; Jacobs et al., 2019). Jacobs et al. (2019) referred the specimen to *Coloborhynchus* based on the position of the first tooth pair on the anterior end of the rostrum, and provided a revised diagnosis for this genus. *Coloborhynchus fluviferox* also bears a shallow, oval depression, ventral to the first tooth pair, as in *Uktenadactylus wadleighi* and *Coloborhynchus capito* (Jacobs et al., 2019). The phylogenetic analysis of Jacobs et al. (2019) supports the close relationship between specimens referred to *Coloborhynchus* and *Uktenadactylus wadleighi*. *Coloborhynchus fluviferox* was subsequently referred to the newly erected genus *Nicorhynchus* by Holgado and Pêgas (2020), with *Coloborhynchus capito* designated the type species. We follow Smith et al. (2022) and regard the minor morphological differences used to assign FSAC-KK 10701 to *Nicorhynchus* of little taxonomic significance and maintain *Coloborhynchus fluviferox* as a valid taxon.

The most recent report of ornithocheirid cranial material is that published by Jacobs et al. (2020), with the description of three fragmentary specimens derived from the Ifezouane Formation. These authors figured and described a partial mandibular symphysis (FSAC-KK 5005), which they regarded as *Anhanguera* cf. *piscator*, based on the morphology of the mandibular crest and dentition. FSAC-KK 5005 is missing the anterior end of the symphysis, and was interpreted as preserving the fourth through ninth tooth pairs on both the left and right ramus (Jacobs et al., 2020). The alveoli on each ramus in FSAC-KK 5005 are laterally offset, such that their relative positions are not bilaterally symmetrical, as in other ornithocheirids such as *Anhanguera piscator*, '*Anhanguera robustus*' and *Ludodactylus sibbicki*. The occlusal surface of FSAC-KK 5005 preserves a mandibular groove which widens posteriorly and develops into a V-shaped depression, flanked by two parallel ridges (Jacobs et al., 2020). As noted by Jacobs et al. (2020) this is not autapomorphic of the *Anhanguera*, with similar occlusal surfaces observed in other members of the Ornithocheiridae. Jacobs et al. (2020) also figured and described two ornithocheirid partial premaxillae held in private collections: *Coloborhynchus* sp. (casts FSACKK 5024 and SMNK PAL 45,833) and *Ornithocheirus* cf. *simus* (casts FSAC-KK 5025, SMNK PAL 45,831). Although Holgado and Pêgas (2020) also referred FSACKK 5024/SMNK PAL 45,833 to *Nicorhynchus fluviferox*, we follow Smith et al. (2022) and regard *Nicorhynchus* a junior synonym of *Coloborhynchus*. Although FSACKK 5024/SMNK PAL 45,833 differs from the *Coloborhynchus fluviferox* holotype, it remains uncertain as to whether these morphological differences are taxonomically significant, or the result of sexual dimorphism or ontogenetic variation (Smith et al., 2022). The taxonomic assignment of *Ornithocheirus* cf. *simus* (casts FSAC-KK 5025, SMNK PAL 45,831) is based on the position of the alveoli and morphology of the rostrum in anterior and lateral views (Jacobs et al., 2020). Additional indeterminate ornithocheirids from the Kem Kem Group include a partial mandibular ramus (FSAC-KK 33) figured and described by Ibrahim et al. (2020), and a partial notarium (FSAC-KK 5208) comprising three anterior centra and possibly a fourth, crushed centrum described by Smith et al. (2022).

Leptostomia begaaensis was established by Smith et al. (2020), based on a partial rostrum (FSAC-KK 5075: holotype) and a partial mandibular symphysis (FSAC-KK 5076: referred), both from the Ifezouane Formation. *Leptostomia* was tentatively regarded as an azhdarchoid, and differs from other members of this clade in that the rostrum is elongate and dorsoventrally narrow (Smith et al., 2020). Referral of *Leptostomia* to the Azhdarchoidea is based on a combination of features, including edentulous jaws, presence of slit-like foramina and relatively thick cortical bone (Smith et al., 2020). Both specimens derive from the?Albian–lower Cenomanian Upper Ifezouane Formation of the Kem Kem Group, and were collected from the mine at Aferdou N'Chaft (Smith et al., 2020). Although there is no anatomical overlap between the holotype and paratype specimens, referral of FSAC-KK 5075 and FSAC-KK 5076 to the same taxon was based on size congruence between the two elements, as well as similarities in cross-sectional profiles and distribution of foramina (Smith et al., 2020). *Leptostomia* is suggested to have been a probe-feeding pterosaur, as the rostrum is dorsoventrally compressed and laterally narrow, with a reduced central cavity when compared with other azhdarchoids (Smith et al., 2020). Unfortunately, the anterior tip is missing in the holotype specimen and referred specimen (FSAC-KK 5076) such that the presence of structures associated with remote sensing (i.e. multiple foramina) cannot be determined (Smith et al., 2020). The rostrum is defined by the presence of a palatal ridge and slightly higher lateral angles ($\sim$2.5°), whereas the mandible possesses a groove on the occlusal surface and lateral angles of $\sim$ 2° (Smith et al., 2022). Although *Leptostomia* was recently resolved within Thalassodromidae by Andres (2021), Smith et al. (2022) regard the former as a non-tapejarid azhdarchoid, as the taxon is known from fragmentary remains with limited characters.

Xericeps curvirostris was described by Martill et al. (2018b) and established based on an edentulous partial mandibular symphysis (FSAC-KK 10700) from the Aoufous Formation. The specimen was purchased by one of the authors from the Aferdou N'Chaft mine site, near the village of Hassi el Begaa in Er Rachidia Province and is interpreted as the mid-section of the symphysis, lacking its anterior tip (Martill et al., 2018b). *Xericeps* differs from other azhdarchoids in that the mandible has a distinct upward curvature (including the occlusal surface), combined with the presence of a distinct groove is located on the ventral surface of the symphysis (Martill et al., 2018b). *Xericeps* also possesses paired, elongate foramina along the occlusal and lateral surfaces, a derived feature of azhdarchoids (Martill et al., 2018b). Although Martill et al. (2018b) regarded *Xericeps* as a non-tapejarid azhdarchoid, more recently it was resolved within Thalassodromidae by Andres (2021). However, referral of *Xericeps* to Thalassodromidae has been questioned by Smith et al. (2022), who note that such an interpretation is based on limited character scores and instead regard *Xericeps* as an indeterminate non-tapejarid azhdarchoid.

Other remains of indeterminate azhdarchoids from the Kem Kem Group include partial jaws, cervical vertebrae, scapulocoracoid, humeri, ulnae, metacarpal IV and a tibiotarsus (Smith et al., 2022). Smith et al. (2022) also regarded the partial mandibular symphysis FSAC-KK 31 (previously referred to *Alanqa saharica* by Ibrahim et al. (2010)) and an incomplete cervical vertebra (FSAC-KK 34; previously regarded as Azhdarchidae indet. by Ibrahim et al. (2010)) as indeterminate azhdarchoids.

Although tapejarid material was first identified from the Kem Kem Group by Wellnhofer and Buffetaut (1999b), the first tapejarid taxon was not established until more than twenty years later (Martill et al., 2020b). *Afrotapejara zouhrii* (FSAC-KK 5004: partial premaxilla) from the Ifezouane Formation was erected by Martill et al. (2020b) based on a combination of features, including the presence of rows of small foramina on the lateral margins of the occlusal surface, and small wedge-shaped protuberance on the preserved posterior end of the occlusal surface. Martill et al. (2020b) also referred two partial rostra (FSAC-KK 5006 and FSAC-KK 5007) from the Kem Kem Group to *Afrotapejara*, and tentatively referred a partial mandibular symphysis (BSP 1997 I 67) to this taxon. BSP 1997 I 67 was previously regarded as a tapejarid by Wellnhofer and Buffetaut (1999b). Averianov (2014b) figured BSP 1997 I 67 as a young ontogenetic stage of *Alanqa saharica*, although this was refuted by Martill et al. (2020b). The referral of FSAC-KK 5006 and FSAC-KK 5007 to *Afrotapejara* was based on their resemblance to the preserved anterior portion of the holotype specimen, whereas the tentative referral of BSP 1997 I 67 is based on size congruence (Martill et al., 2020b). As mentioned earlier, MN 7054-V was first interpreted as a pteranodontid mandibular symphysis by Kellner et al. (2007a), was subsequently regarded as a tapejarid rostrum by Ibrahim et al. (2020), and most recently referred to *Afrotapejara zouhrii* by Smith et al. (2022). Additional specimens referred to *Afrotapejara* include three indeterminate jaw fragments (FSAC-KK 29, FSAC-KK 32 and UCRC PV 161; Smith et al., 2022). Smith et al. (2022) also provided a revised diagnosis of *Afrotapejara*, such that the taxon can be distinguished from other tapejarids based on the presence of two rows of small foramina on the lateral margins of the rostrum. Based on the phylogenetic analysis conducted by Martill et al. (2020b), *Afrotapejara* is resolved as a derived tapejarid in a polytomy with *Tapejara*, *Europejara* and *Tupandactylus*.

At present, *Apatorhamphus gyrostega* (FSAC-KK 5010, cast UOP-PAL-KK0001) constitutes the only chaoyangopterid from Africa, and indeed, Gondwana, and is represented by regarded as a partial probable premaxilla, missing its anterior end (McPhee et al., 2020). In addition to the holotype specimen of *Apatorhamphus*, McPhee et al. (2020) identified five referred specimens, including FSAC-KK 5011, FSAC-KK 5012, FSAC-KK 5013 (also collected from Begaa) and FSAC-KK 5014 (locality unknown). The fifth referred specimen, BSP 1993 IX 338, was first described by Wellnhofer and Buffetaut (1999a) as a pteranodontid and later regarded as *Alanqa saharica* by Ibrahim et al. (2010). McPhee et al. (2020) noted that BSP 1993 IX 338 is morphologically congruent with the *Apatorhamphus* holotype specimen, and regarded subtle differences in the lateral margins as the result of ontogenetic variation. By contrast, assignment of the other referred specimens to *Apatorhamphus* was based on gross morphology, as well as cross-sectional shape (McPhee et al., 2020). Referral of *Apatorhamphus* to the Chaoyangopteridae is because of the presence of a straight occlusal surface, and gently concave dorsal margin (McPhee et al., 2020). Placement within the Chaoyangopteridae is further supported by the recent phylogenetic analysis of Andres (2021).

Although several edentulous taxa are known from the Kem Kem Group, at present, the only azhdarchid taxon is *Alanqa saharica*, erected based on FSAC-KK 26, a mandibular symphysis (Ibrahim et al., 2010). Several other jaw fragments have been referred to this taxon, including the anterior-most portion of a premaxilla (BSP 1996 I 36; previously regarded as an indeterminate azhdarchid by Wellnhofer & Buffetaut 1999) and FSAC-KK 27, a rostral element (Ibrahim et al., 2010). Ibrahim et al. (2010) also referred BSP 1993 IX 338 and BSP 1996 I 36 to *Alanqa saharica*; however, the referral of BSP 1996 I 36 to *Alanqa saharica* has been questioned by Martill and Ibrahim (2015), who noted similarities in morphology between the former and the *Alanqa saharica* holotype (FSAC-KK 26), interpreting both as rostral elements. Similarly, BSP 1993 IX 338 was subsequently referred to the newly erected chaoyangopterid *Apatorhamphus gyrostega* by McPhee et al. (2020), based on similarities between it and the *Apatorhamphus* holotype (FSAC-KK 5010). Additional specimens referred to *Alanqa saharica* include a partial symphysial mandible (FSAC-KK 4000; Martill and Ibrahim, 2015), two partial rostra (FSAC-KK 5204 and FSAC-KK 5205), a partial mandibular symphysis (FSAC-KK 5213/ UOP-PAL-KK 0006) and indeterminate jaw fragments (BSP 1996 I 36; FSAC-KK 4002, 5078, 5079, 5080; Smith et al., 2022).

Postcranial remains attributed to indeterminate azhdarchids include that of a large cervical vertebra (LINHM 014; Kellner and Mader, 1996). LINHM 014 was more recently figured and described by Rodrigues et al. (2011) who noted remnants of fused cervical ribs, indicating a subadult or osteologically mature individual. LINHM 014 is anteroposteriorly elongate, has a dorsoventrally short neural spine (as is typical of azhdarchid cervical vertebrae), and has two large pneumatic openings positioned lateral to the neural canal, visible on both the anterior and posterior surfaces (Rodrigues et al., 2011). Additional isolated, postcranial azhdarchid remains include several cervical vertebrae (CMN 50801; FSAC-KK 3088, 5077, 5083, 5214–5216, 5218 and 7251), notarium (FSAC-KK 5207), wing phalanx (FSAC-KK 5212) and femur (FSAC-KK 7141; Smith et al., 2022).

Possible pterosaur manus tracks have been reported from the Kem Kem Group by Belvedere et al. (2013). As in other pterosaur manus tracks, digit I is positioned anteriorly and short, whereas digit III is the longest and directed laterally (Belvedere et al., 2013). Given that the tracks are poorly preserved and do not form a trackway, Belvedere et al. (2013) did not assign these to an ichnotaxon.

4.2.9. Turkana Grits, Kenya

An isolated and heavily-abraded cervical vertebra comprising fused centrum and neural arch (KNM-WT 47893) was reported from the Upper Cretaceous Turkana Grits (Lapurr Sandstone) of West Turkana, northwestern Kenya (O'Connor et al., 2011). A Turonian–lower Campanian age is suggested for the Lapurr sandstone, based on comparisons with subsurface geology, as well as the fossil

assemblage (O'Connor et al., 2011). KNM-WT 47,893 was tentatively classified within Azhdarchidae, on the basis of an absence of pneumatic foramen on the centrum and neural arch (O'Connor et al., 2011).

4.2.10. Western high Atlas, Morocco

The Coniacian-Santonian Anza Tracksite preserves eleven pterosaur manus tracks and a manus-only trackway comprising asymmetric tridactyl prints in calcareous sandstone (Lkebir et al., 2020b; Masrour et al., 2017). The Anza pterosaur tracks are similar to the *Agadirichnus* and *Pteraichnus* pterosaur ichnotaxa (Lkebir et al., 2020a; Lkebir et al., 2020b; Masrour et al., 2017).

4.2.11. Paki Formation, Senegal

To date, the only pterosaur remains reported from the Campanian Paki Formation in the Basin of Senegal are an elongate cervical vertebra and partial tibia (Monteillet et al., 1982). The specimen number of both the cervical vertebra and tibia is not known. Although Monteillet et al. (1982) regarded these remains as an indeterminate azhdarchid, as the tibia does not possess any diagnostic features, Kellner et al. (2007a) interpreted it as an indeterminate pterodactyloid.

4.2.12. Logbadjeck Formation, Cameroon

Indeterminate pterosaur remains have been reported from the lower Campanian Logbadjeck Formation of Cameroon (Ntamak-Nida et al., 2006). This material awaits formal description.

4.2.13. Mocuio Formation, Angola

A partial femur (MGUAN-PA163; the specimen number was incorrectly given as MGUN-PA163) was reported from the Lower Maastrichtian Mocuio Formation of Angola by Mateus et al. (2012). The specimen is represented by part of the femoral head and much of the diaphysis, but the medial surface of the femoral head and much of the greater trochanter is missing.

More recently, Fernandes et al. (2022) described new material from the Lower Maastrichtian of Angola, including a new taxon, *Epapatelo otyikokolo* known from two individuals. *Epapatelo* was established based on the distal end of a left humerus and complete left ulna found in articulation (MGUAN-PA650), and a referred specimen represented by a left ulna and radius (MGUAN-PA661; Fernandes et al., 2022). Phylogenetic analysis resolved *Epapatelo* as a non-nyctosaurid pteranodontian in a trichotomy with *Simurghia robusta* and *Alcione elainus* (Fernandes et al., 2022). Additional indeterminate pterosaur remains mentioned by Fernandes et al. (2022) include the proximal end of a left third wing phalanx (MGUAN-PA652), the distal end of a right ulna (MGUAN-PA653), the distal end of a left second wing phalanx (MGUAN-PA656), the proximal end of a left first wing phalanx (MGUAN-PA657), a limb shaft (MGUAN-PA658) and a left first wing phalanx (MGUAN-PA659; Fernandes et al., 2022). Other remains mentioned by Fernandes et al. (2022) include an indeterminate pterodactyloid represented by the proximal end of a right metacarpal IV (MGUAN-PA660), and an indeterminate pteranodontian comprising the distal end of a right metacarpal IV and the proximal end of a right first wing phalanx (MGUAN-PA654). Fernandes et al. (2022) also regarded MGUAN-PA163 (a left femur tentatively referred to the Ornithocheiroidea by Mateus et al. (2012)) as a pteranodontian, based on the deflection of the femoral head relative to the shaft.

4.2.14. Oulad Abdoun Basin, Morocco

The third partial pterosaur skeleton from the African Cretaceous is the azhdarchid *Phosphatodraco mauritanicus* (OCP DEK/GE 111; Pereda Suberbiola et al., 2003). The holotype specimen represented by a series of cervical vertebrae recovered from the upper Maastrichtian phosphatic deposits from the Oulad Abdoun Basin, Morocco. Pereda Suberbiola et al. (2003) originally interpreted these as five cervical vertebrae, specifically V-IX; however, Kellner (2010) observed that the first vertebra in this specimen comprises two broken cervical elements preserved together, with the holotype preserving cervical vertebrae III-VII. As stated by Kellner (2010), while this does not impact the taxonomic status of *Phosphatodraco*, the diagnosis needs revision and the estimated wingspan of this taxon should be reduced accordingly. Additional material referred to *Phosphatodraco* includes the cervical vertebrae FSAC-OB 12 (cervical vertebra V) and FSAC-OB 13 (position within cervical series unknown; Longrich et al., 2018). It should be noted that Longrich et al. (2018) based comparisons on the revised interpretation of Kellner (2010), wherein the holotype specimen comprises six cervical vertebra.

The description of postcranial remains derived from the upper Maastrichtian 'Couche III' layer of the phosphatic deposits in the Oulad Abdoun Basin in the Khouribga Province of central Morocco hints at moderate levels of diversity in edentulous pterosaur taxa. Longrich et al. (2018) erected four taxa from the phosphatic layer informally referred to as 'Couche III', including three nyctosaurids *Simurghia robusta* (FSAC-OB 7), *Alcione elainus* (FSAC-OB 2) and *Barbaridactylus grandis* (FSAC-OB 232). The fourth taxon, *Tethydraco regalis* (FSAC-OB 1), erected based on a left humerus, was initially regarded as a pteranodontid by Longrich et al. (2018), but was subsequently reallocated to the Azhdarchidae by Labita and Martill (2021). The holotype and only known specimen of *Simurghia robusta* is a humerus (FSAC-OB 7), regarded as a large-bodied nyctosaurid comparable in size and morphology to '*Nyctosaurus*' *lamegoi* (Longrich et al., 2018). Although the *Simurghia* holotype is incomplete distally, Longrich et al. (2018) noted that a large, subtriangular supracondylar process is autapomorphic for this taxon, distinguishing it from other nyctosaurids. By contrast, *Alcione elainus* is interpreted as a small-bodied nyctosaurid, known from multiple individuals, with the holotype specimen, FSAC-OB 2, comprising postcranial elements including the sternum, scapulocoracoid, humerus and femur (Longrich et al., 2018). Material referred to this taxon includes a partial wing comprising humerus, radius, ulna, as well as partial metacarpal IV and first wing phalanx (FSAC-OB 4), metacarpal IV (FSAC-OB 217) and fragmentary mandible (FSAC-OB 156; Longrich et al., 2018). Longrich et al. (2018) noted considerable variation in the morphology of the deltopectoral crest of adult individuals attributed to *Alcione*, postulating that this might be because of individual variation, or that this taxon may not be monospecific. The third nyctosaurid taxon erected by Longrich et al. (2018) is *Barbaridactylus grandis* (FSAC-OB 232) was established based on a partial skeleton, comprising partial right mandibular ramus, left scapulocoracoid, left humerus, radius and ulna and right femur. *Barbaridactylus* differs from other members of the Nyctosauridae in possessing a quadrangular deltopectoral crest (Longrich et al., 2018). *Barbaridactylus* also differs from other nyctosaurids in that pneumatic foramina or a single pneumatic foramen is located on the anterior surface, distal to the deltopectoral crest (Longrich et al., 2018). Other material figured and described by Longrich et al. (2018) includes two elongate cervical vertebrae (FSAC-OB 12 and FSAC-OB 13), both referred to *Phosphatodraco mauritanicus* based on their relative proportions; a dorsoventrally compressed cervical vertebra (FSAC-OB 14) regarded as an azhdarchid aff. *Quetzalcoatlus*; and a left ulna of a large azhdarchid, represented by the diaphysis and distal end (FSAC-OB 203; Longrich et al., 2018). As well as describing and figuring the aforementioned specimens, Longrich et al. (2018:table S1) mentioned other referred specimens of the four, newly described taxa as well as, various indeterminate remains.

More recently, a partial articulated wing (FSAC CP 251) from the upper Maastrichtian 'Couche III' layer was figured and described by Labita and Martill (2021). The partial right wing preserves the

humerus, ulna, radius, carpal elements, metacarpal IV, first wing phalanx and the proximal end of the second wing phalanx (Labita and Martill, 2021). Labita and Martill (2021) referred FSAC CP 251 to *Tethydraco*, based on the morphology of the humerus; however, the deltopectoral crest of the humerus of FSAC CP 251 is hatchet-shaped, and thus differs from the *Tethydraco* holotype. Labita and Martill (2021) noted that a hatchet-shaped deltopectoral crest is typical of azhdarchids and postulated that the curved deltopectoral crest observed in the *Tethydraco* holotype specimen might be because of crushing. Given that the biometric ratios of FSAC CP 251 are consistent with members of the Azhdarchidae, Labita and Martill (2021) subsequently regarded *Tethydraco* as an azhdarchid, and not a pteranodontid *contra* Longrich et al. (2018). Moreover, Labita and Martill (2021) also noted that as *Phosphatodraco mauritanicus* is known solely from cervical vertebrae, *Tethydraco* might in fact represent the wing elements of *Phosphatodraco* and thus be a junior synonym.

4.2.15. Tagragra Formation, Morocco

At present, pterosaurs are only known from the Maastrichtian Tagragra Formation, based on isolated pterosaur manus and pes tracks (Ambroggi and De Lapparent, 1954; Masrour et al., 2018). Isolated pterosaur manus prints (FSA.G.51) and associated manus and pes tracks (FSA.G.52) were regarded as cf. *Pteraichnus* isp., whereas other isolated tracks were referred to *Agadirichnus elegans* (FSA.G.54 - FSA.G.57), demonstrating the latter is a pterosaurian ichnotaxa (Masrour et al., 2018).

5. Arabian Peninsula

Although presently part of Asia, during the Mesozoic the Arabian Peninsula was part of the African continent (Philip et al., 1993; Saint-Marc, 1978). At present, pterosaur remains have been reported exclusively from the Cretaceous at localities across Israel, Jerusalem, Jordan and Lebanon.

5.1. Ein-Yabrud, Jerusalem

A partial pterosaur (lacking specimen number) was mentioned but not figured by Polcyn et al. (1999) from the lower Cenomanian Ein Yabrud near Jerusalem. Housed at the Hebrew University of Jerusalem, the specimen was collected by quarry workers along with dozens of other fossils including fish, snakes, turtles, mosasauroids, lizards, ammonites, echinoderms, bivalves and crustaceans (Polcyn et al., 1999). As stated by Kellner et al. (2007a), the specimen comprises an isolated hind limb and awaits formal description.

5.2. Hâqel Lagerstätte, Lebanon

The first pterosaur reported from Lebanon comprises a partial forelimb (MSNM V 3881) derived from the lower Cenomanian Hâqel marine Lagerstätte (Dalla Vecchia et al., 2001). The forelimb preserves the distal end of the humerus, ulna, radius, carpals, metacarpals I-IV, wing phalanges, manual claws and the proximal end of wing phalanx 1 (Dalla Vecchia et al., 2001). Based on the fusion of the carpals, and the fusion of the extensor tendon process to the first wing phalanx, MSNM V 3881 represents an osteologically mature individual (Dalla Vecchia et al., 2001).

5.3. Hjoûla Lagerstätte, Lebanon

The most complete pterosaur from the Arabian Peninsula, *Mimodactylus libanensis* (MIM F1) was reported by Kellner et al. (2019a) and derives from the upper Cenomanian Sannine Limestone (~95 mya) of the Hjoûla *Lagerstätte*, Lebanon. The holotype specimen preserves the anterior portions of the upper and lower jaws, some cervical vertebrae, dorsal vertebrae, dorsal ribs, caudal vertebrae, both wings and part of the hind limb (Kellner et al., 2019a). As with other specimens recovered from the *Lagerstätten* of Lebanon, all elements are closely associated and some elements of the wing (specifically, the wing phalanges) are preserved in articulation (Kellner et al., 2019a). *Mimodactylus* was referred to the newly erected clade, the Istiodactyliformes, defined as the most inclusive clade containing *Istiodactylus latidens*, but not *Anhanguera blittersdorffi* (Kellner et al., 2019a). As noted by Kellner et al. (2019a), *Mimodactylus* differs from other specimens described from the Hjoûla *Lagerstätte*, based on the proportions of elements of the wing, and when compared with *Microtuban*, the morphology of the deltopectoral crest of the humerus. The cranial material of *Mimodactylus* shows a mosaic of features (Kellner et al., 2019a). This includes cone-shaped teeth confined to the anterior part of the skull, odontoid process positioned at the anterior end of the lower jaw, dentition characterised by a cingulum basal to each crown, but lacks the sharp carinae typical of *Istiodactylus* (Kellner et al., 2019a). Kellner et al. (2019a) noted that the unique dentition of *Mimodactylus* is reminiscent of basal archaeopterodactyloids, and speculated that *Mimodactylus* was predominantly insectivorous, or alternatively, adapted to feed on shrimp or decapod crustaceans.

A partial postcranial skeleton reported from the upper Cenomanian Hjoûla *Lagerstätte* (Sannine Formation) was used to establish the azhdarchoid taxon *Microtuban altivolans* (SMNK PAL 6595; Elgin and Frey, 2011b). The holotype and only known specimen of *Microtuban* comprises axial and appendicular elements, specifically, the posteriormost cervical and anteriormost dorsal vertebrae, a complete left wing, pectoral girdle and fragmentary hind limbs (Elgin and Frey, 2011b). Elgin and Frey (2011b) interpreted *Microtuban* as an azhdarchoid, based on the presence of a well-developed tubercle on the posteroventral margin of the coracoid, elongation of the first wing phalanx (representing more than 40% the length of the wing finger) and reduction of the fourth wing phalanx. Several elements in the *Microtuban* holotype specimen are unfused, including the scapula and coracoid, as well as the cervical and thoracic ribs relative to the vertebrae (Elgin and Frey, 2011b). Although the extensor tendon process is fused to the first wing phalanx, a large suture was identified between the two, indicating that the *Microtuban* holotype is either a juvenile or subadult individual (Elgin and Frey, 2011b). Initially, *Microtuban* was tentatively regarded as a member of the Thalassodromidae or Chaoyangopteridae (Elgin and Frey, 2011b). More recently, *Microtuban* has been more recently resolved within the Azhdarchoidea but outside Dsungaripteridae by Andres (2021).

5.4. Mishash Formation, Israel

The first report of pterosaur remains from Israel was made by Lewy et al. (1992) and comprised two endocranial casts, the proximal end of a humerus and wing phalanges from the upper Campanian Phosphate Member of the Mishash Formation. The most complete endocast (M−8047/1649) is incomplete ventrally, but the dorsal and lateral surfaces remains intact; nevertheless, it is clear that the olfactory bulb was reduced, whereas the cerebellum, particularly the floccular lobes were well developed (Lewy et al., 1992). Both endocasts were tentatively assigned to the azhdarchid *Arambourgiania* on the basis of their spatial proximity to isolated remains of the same taxon, and the fact that both localities had similar palaeoenvironments (Lewy et al., 1992). The appendicular elements and less complete endocast lack specimen numbers.

5.5. Phosphate Deposits, Jordan

A putative wing metacarpal (VF 1) indicating a giant pterosaur from Maastrichtian phosphate deposits near Ruseifa in Jordan was mentioned by Arambourg (1954), who erected the taxon *Titanopteryx philadelphiae*. Lawson (1975) later identified VF 1 as a cervical vertebra, an interpretation which has since been widely accepted (Frey and Martill, 1996; Kellner et al., 2007a). Nesov et al. (1987) suggested the generic name *Arambourgiania* upon discovering *Titanopteryx* was preoccupied. *Arambourgiania philadelphiae* was considered a *nomen dubium* by Bakhurina and Unwin (1995) on the basis that the holotype did not possess any diagnostic features at the generic level (Frey and Martill, 1996). However, the taxonomic validity of *Arambourgiania* was supported by Frey and Martill (1996), who designated the plaster replica BSP 1978/1 as the neotype. The whereabouts of the *Arambourgiania* holotype (VF 1) remained a mystery for several years, until Frey and Martill (1996) located the lost specimen at the University of Jordan with assistance from Mr Tawfiq Amin Kawar and Dr Rushdie Sadaqah (Martill and Moser, 2018). Frey and Martill (1996) also described new material from the same stratigraphic horizon and locality as the holotype: a smaller cervical vertebra (SMNK 1285 PAL), the proximal end of the first wing phalanx (SMNK 1286 PAL), and the distal end of the first wing phalanx (SMNK 1287 PAL); all referred to *Arambourgiania philadelphiae*. The three specimens were previously on display at the office of the Jordan Phosphate Mining Company in Ruseifa, Jordan (Martill and Moser, 2018). More recently, additional material from the Maastrichtian of phosphate deposits of Ruseifa, Jordan was figured and described by Martill and Moser (2018), including axial and appendicular elements. This includes the proximal end of a left metacarpal IV (SNSB-BSPG 1966 XXV 501), partial cervical vertebrae (SNSB-BSPG 1966 XXV 503 and 508), proximal end of the left femur (SNSB-BSPG 1966 XXV 506), possible distal end of a radius (SNSB-BSPG 1966 XXV 507), and fragmentary neural arch (SNSB-BSPG 1966 XXV 512). Although no definitive azhdarchid autapomorphies were identified, Martill and Moser (2018) referred the material to the Azhdarchidae, based on the elongate cervical vertebra with medially positioned neural canal and relatively thick cortical bone (ca. 2 mm). As stated by Martill and Moser (2018), there is no anatomical overlap between the material described by those authors, the three elements described by Frey and Martill (1996), or the holotype cervical vertebra (VF 1) described by Arambourg (1954). Unfortunately, a lack of field data means that it cannot be determined with certainty if all of the material can be attributed to the same individual (Frey and Martill, 1996; Martill and Moser, 2018). More recently, putative remains of two azhdarchid pterosaurs were reported from the Maastrichtian of Jordan, with one specimen referred to *Arambourgiania philadelphiae* (Rosenbach et al., 2018). The other specimen represents a much smaller azhdarchid (wingspan $\sim$ 5 m) and was provisionally regarded as a new taxon but awaits formal description and is regarded here as Azhdarchidae indet. (Rosenbach et al., 2018). Micro-computed tomography (μCT) scans of the humeri demonstrated the internal struts in the larger specimen were arranged helically, whereas in the smaller specimen, these struts had a denser distribution (Rosenbach et al., 2018). Interestingly, X-ray CT scans have demonstrated that the internal cross struts in the cervical vertebrae of *Alanqa* sp. from the Kem Kem Group of Morocco were also arranged helically (Williams et al., 2021).

5.6. Muwaqqar Chalk Formation, Jordan

To date, pterosaur remains have been reported from the uppermost Maastrichtian Muwaqqar Chalk Formation (Harrana Fauna; Kaddumi, 2009) but await formal description. One such specimen, ERMNH HFV 227, was regarded as a nyctosaurid based on the morphology of the first wing phalanx (Kaddumi, 2009). Other specimens include an ulna and first wing phalanx (Kaddumi, 2009), as well as an incomplete but well-preserved notarium also mentioned by Kaddumi (2006).

6. Madagascar

6.1. Mahajanga Basin, Madagascar

The first pterosaur material reported from Madagascar includes four teeth (MSNM V5170- 5173) from the Middle Jurassic (Bathonian) Isalo III Formation in the Mahajanga Basin (Dal Sasso and Pasini, 2003). Two morphotypes were identified, with all four teeth tentatively referred to the Rhamphorhynchoidea (Dal Sasso and Pasini, 2003). Affinities to either *Angustinaripterus* or *Rhamphocephalus* were suggested, on the basis of their similar size and morphology (Dal Sasso and Pasini, 2003). If correct, the teeth suggest the presence of a medium-sized non-pterodactyloid pterosaur in the Jurassic of Madagascar (Dal Sasso and Pasini, 2003).

6.2. Morondava Basin, Madagascar

Putative pterosaurian remains comprising the distal end of an ulna and radius have been recovered from a concretion derived from the Campanian Morondava Basin of western Madagascar (Burch and Sertich, 2011). On the basis of size and morphology, the material was tentatively referred to the Azhdarchidae, with the dorsal articular surface of the ulna comparable to that of *Azhdarcho lancicollis* (Burch and Sertich, 2011). These remains await formal description.

7. Indo-Pakistan subcontinent

7.1. Kota Formation, India

The majority of pterosaur remains reported from India derive from the lowermost beds of the Lower–Middle Jurassic (Prasad and Manhas, 2007) Kota Formation (Rao and Shah, 1963). This includes one of the earliest reports of pterosaur remains from India, those of postcranial remains ('No. K 49 / 884, also known as GSI type No. 17,868 or GSI 17868) recovered from a limestone ledge near Chitur (Rao and Shah, 1963). GSI 17868 comprises an ulna, radius, wing metacarpal, first wing phalanx and pedal phalanx and was assigned to *Rhamphorhynchus* (Rao and Shah, 1963). These remains were later referred to '*Campylognathoides indicus*' by Jain (1974); however, the pterosaurian affinities of the material has been questioned. In their original description Rao and Shah (1963) also noted the presence of dermal ossifications, a feature not known in any pterosaur. The suggestion that these dermal ossifications may belong to a fish, proposed by Padian (2008a), is supported here. The assignment of GSI 17868 to *Rhamphorhynchus* was first questioned by Colbert (1969), and as noted by Padian (2008a) the ratio of the preserved forearm to first wing phalanx (=1.17) of GSI 17868 does not conform to those of *Campylognathoides* (2.3–3; Padian, 2008a). Given that GSI 17868 does not possess any synapomorphies, it was most recently regarded as an indeterminate pterosaur (Padian, 2008a).

The first pterosaur taxon reported from India, '*Campylognathoides indicus*', was established based on the anterior portion of a skull bearing three premaxillary teeth (ISI R 48), by Jain (1974). Jain (1974) also referred three carpal elements (ISI R 49) and GSI 17868 to '*Campylognathoides indicus*', despite a lack of anatomical overlap between the three specimens. The '*Campylognathoides indicus*' holotype specimen (ISI R 48) possesses several

characters not observed in *Campylognathoides*, including a long toothless premaxillary tip, grooved teeth and long posterior process beneath the naris (Padian, 2008a). Similarly, as ISI R 48 lacks affinities with the *Campylognathoides*, and for that matter the Pterosauria, Padian (2008a) suggested it may in fact belong to a fish. This interpretation was supported by Alarcón-Muñoz et al., (2021) who regarded '*Campylognathoides indicus*' as an indeterminate member of Osteichthyes.

7.2. Samana Suk Limestone, Pakistan

The geologically oldest pterosaur tracks reported from Indo-Pakistan are from the Late Jurassic Samana Suk limestone, from Moharian (Salt Range), north of Quidabad (Malkani, 2021). These tracks were referred to the ichnotaxon *Haenamichnus* from South Korea (Malkani, 2019), which have been attributed to an azhdarchid (Hwang et al., 2002). However, given that large pterosaurs (wingspans greater than 2 m) are rare in the Late Jurassic, it is unlikely that the Samana Suk limestone tracks can be attributed to an azhdarchid or referred to this ichnotaxon.

7.3. Lameta Formation, India

The first pterosaur material reported from India includes a jaw fragment containing three teeth and two unoccupied alveoli (lacking specimen number; Dubey and Narain, 1946). The provisional assigment to the Pterosauria was based on the closely-spaced, apically blunt, slender, conical teeth, which were interpreted as insectivorous dentition, and preservation in arenaceous and silicified shale deposited in a lacustrine setting (Dubey and Narain, 1946). The pterosaurian affinities of the material described by Dubey and Narain (1946) has been questioned by Colbert (1969), Jain (1974) and Dalla Vecchia et al. (2013). At the time of the publication of Dubey and Narain (1946), the specimen was sent to the British Museum for further examination. As stated by Dalla Vecchia et al. (2013), given that there is little indication that the specimen is deposited at the British Museum, the current whereabouts of the specimen are not known. According to Barrett et al. (2008) and Dalla Vecchia et al. (2013), the specimens described by Dubey and Narain (1946) are Maastrichtian in age, most likely derived from the Intertrappean Beds. By contrast, Malkani (2019) indicated the material described by Dubey and Narain (1946) is from the Maastrichtian Lameta Formation. Given that dentulous pterosaurs are not known from the Maastrichtian, and in the absence of features which would otherwise support its assignment, we follow Dalla Vecchia et al. (2013) such that jaw fragment is not a Maastrichtian pterosaur.

7.4. Vitakri Formation, Pakistan

A fragmentary dentary ramus (MSM-157–16) bearing eight alveoli derived from the latest Maastrichtian Vitakri Formation of Pakistan was interpreted as a pterosaur by Malkani (2013), who erected the taxon '*Saraikisaurus minhui*' (Malkani, 2021). The pterosaur material originally described by Dubey and Narain (1946) from the Lameta Formation was also referred to this taxon by Malkani (2019). Although the author has clearly indicated their intention to establish new names, '*Saraikisaurus minhui*' is not registered with ZooBank (the ICZN online registration system). To complicate matters, the phylogenetic position of '*Saraikisaurus*' within Pterodactyloidea has not been assessed, as the taxon has not been included in a phylogenetic analysis. Given that the latest Cretaceous of Gondwana is dominated by the edentulous azhdarchids, the pterosaurian affinities of this dentulous jaw fragment seems doubtful. Alternatively, MSM-157–16 might represent an element derived from the Early Cretaceous, which was subsequently reworked into latest Cretaceous strata; or, the locality from which MSM-157–16 derives is not Late Cretaceous in age. Nevertheless, the morphological features used to support the identification of MSM-157–16 as pterosaurian (i.e. suboval alveoli and pneumatic texture; Malkani, 2020) are those shared with other vertebrate clades. Moreover, as '*Saraikisaurus minhui*' was established based on non-diagnostic material and in the absence of any autapomorphic features, '*Saraikisaurus minhui*' is regarded here as a *nomen dubium*.

Pterosaur tracks have also been reported from the from the uppermost Maastrichtian Vitakri Formation of Zhob, specifically, from the Sor Muzghai ichnosite (also referred to as the Sur Muzghai site; Malkani, 2018). Malkani (2018) noted that the pterosaur tracks from the Sor Muzghai ichnosite were similar to *Haenamichnus* from the Upper Cretaceous Haman Formation (Changseon and Sinsu Islands, South Korea). A trackway comprising four consecutive manus and pes prints (GSP/MSM-12-Musaferpur), was designated the holotype of the ichnogenus and species '*Anmolpakhi alleni*' (Malkani, 2019; Malkani, 2021). It is unclear how '*Anmolpakhi alleni*' differs from other pterosaur ichnogenera, as there is little information available regarding the relative width of the heel, absence or presence of specific digits or the length of these digits. Moreover, information regarding the stride length, trackway width, pace angulation — or indeed any other trackway measurements — is not available. Referred material includes two tracks from the same site (GSP/MSM-13-Musaferpur and GSP/MSM-14-Musaferpur; Malkani, 2021).

8. Australia

8.1. Eumeralla Formation

Although no pterosaur specimens have been formally described from Victoria, two elements—both recovered from the 'Dinosaur Cove' site—have been mentioned in technical articles (Poropat et al., 2018) and illustrated in popular books (Rich and Vickers-Rich, 2000; Rich and Vickers-Rich, 2020). These elements derive from the upper Aptian–lower Albian Eumeralla Formation (Wagstaff and McEwen Mason, 1989). A purported pterosaur tibiotarsus (NMV P186084) was mentioned by Rich and Rich (1989) and figured by Rich and Vickers-Rich (2000, pl. 14), labelled as a bone "from either the hand or foot". This was later reinterpreted by Bennett and Long (1991) as a crushed metatarsal, and was mentioned by Fletcher and Salisbury (2010), who incorrectly reported the specimen number as NMV P185861. The specimen is labelled as a "wing metacarpal" in the NMV collections (AHP and SFP, pers. observ.).

A partial pterosaur sacrum (NMV P185973) was also discovered at the 'Dinosaur Cove' site, and figured by Rich and Vickers-Rich (2000, pl. 14) and Poropat et al. (2018). At present, pterosaur pelvic characters have not been included within any phylogenetic analysis (Hyder et al., 2014). Fletcher and Salisbury (2010) also made mention of this specimen, but incorrectly gave the specimen number as NMV P197962 and incorrectly stated that it derived from the Upper Strzelecki Group (it is from the Eumeralla Formation).

8.2. Toolebuc Formation

The earliest report of indisputable pterosaur material from Australia, made by Molnar and Thulborn (1980), was based on isolated remains from the upper Albian Toolebuc Formation of central Queensland. Provided were descriptions for a left scapulocoracoid (QM F10612), a presacral vertebra (QM F10614), and a partial mandibular symphysis (QM F10613, now the holotype of *Aussiedraco molnari*). In QM F10612 (Fig. 2A–C), the scapula and

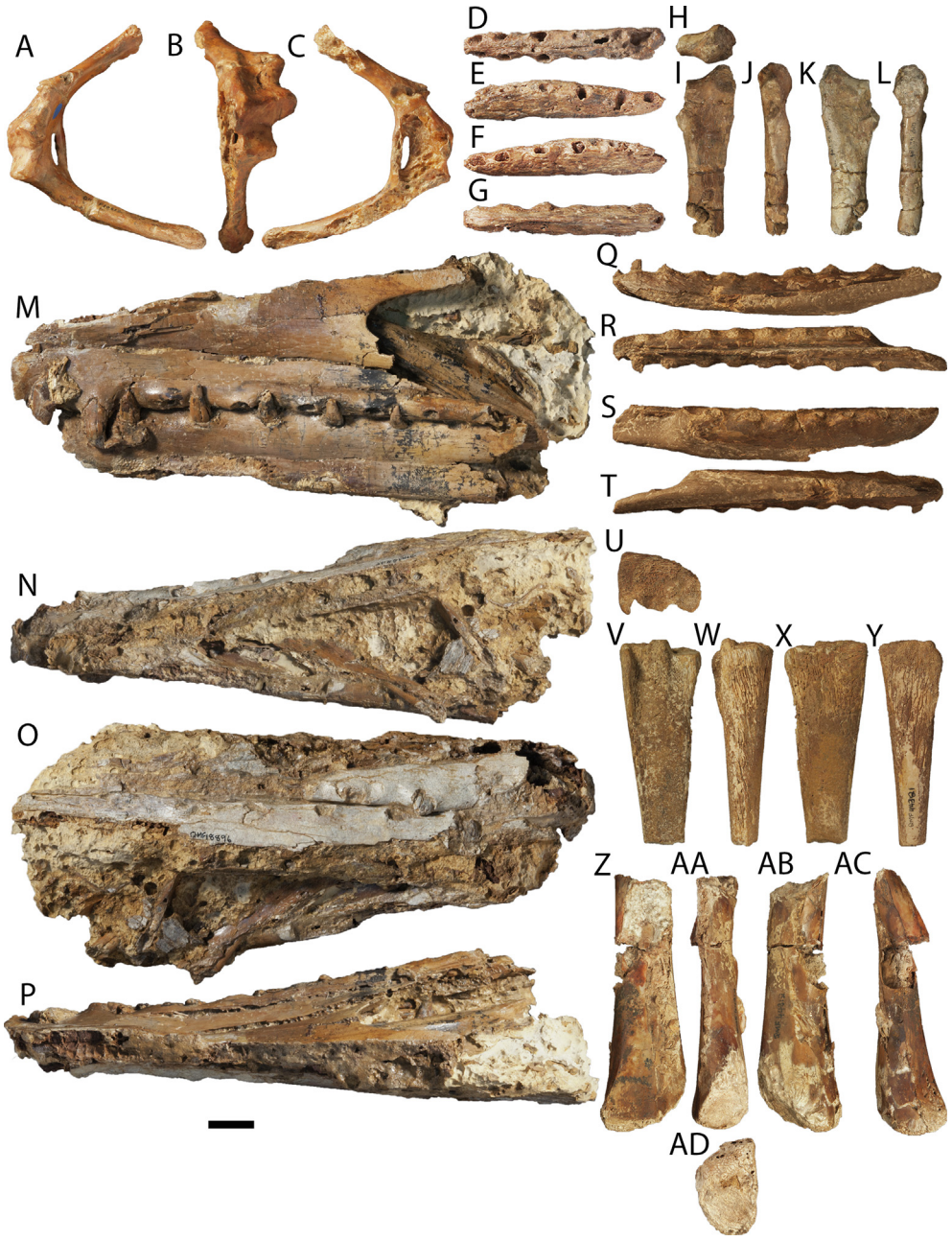

Fig. 2. Isolated pterosaur remains from Queensland, Australia. **A–C,** left scapulocoracoid, QM F10612 in **A,** posterior, **B,** lateral and **C,** anterior views. **D–G,** *Aussiedraco molnari* holotype QM F10613 in **D,** dorsal, **E,** right lateral, **F,** left lateral, and **G,** ventral views. **H–L,** partial left humerus, QM F42739 in **H,** proximal, **I,** anterior, **J,** ventral, **K,** posterior and **L,** dorsal views. **M**–**P,** *Mythunga camara* holotype QM F18896 in **M,** left lateral, **N,** ventral, **O,** right lateral and **P,** dorsal views. **Q–T,** partial mandibular symphysis QM F44423 in **Q,** left lateral, **R,** dorsal, **S,** right lateral and **T,** ventral views. **U–Y,** proximal end of a left metacarpal IV, QM F44321 in **U,** proximal, **V,** anterior, **W,** dorsal, **X,** posterior, and **Y,** ventral views. **Z–AD,** distal end of a left wing phalanx, QM F44312 in **Z,** dorsal, **AA,** posterior, **AB,** ventral, **AC,** anterior and **AD,** distal views. All photographs taken by S.F. P. Scale bar equals 20 mm.

coracoid are fused, indicating an osteologically mature pterosaur; this specimen was regarded as pteranodontid by Molnar and Thulborn (1980), but later regarded as a taxon related to *Anhanguera* by Molnar and Thulborn (2007) (the specimen number was incorrectly given as QM F10613). The Toolebuc scapulocoracoid possesses a coracoid that is larger than the scapula (Kellner, 2003a,b). The suboval form of the proximal (glenoid) articulation surface suggests a pteranodontoid (Kellner, 2003a,b); in more plesiomorphic taxa, the glenoid articular face is more elongate in form (Molnar and Thulborn, 2007). The scapulocoracoid bears some resemblance to *Pteranodon* (Eaton, 1910) and *Anhanguera* (Wellnhofer, 1988, 1991b) in possessing a posterior process and a 'bridge' between the scapula and coracoid (Molnar and Thulborn, 1980). On the basis of the general form of the glenoid, QM F10612 bears resemblance to *Anhanguera santanae* (AMNH 22555), with the V-shaped fossa of the dorsolateral surface of the scapula located between the posterior process and anterior moiety of the scapula (Molnar and Thulborn, 2007). The ratio of the preserved scapula to coracoid length is approximately 0.8 (Molnar and Thulborn, 2007). Given the unique combination of characters, the most parsimonious conclusion is that QM F10612 represents a species closely related to members of the Ornithocheiridae as previously stated by Molnar and Thulborn (2007).

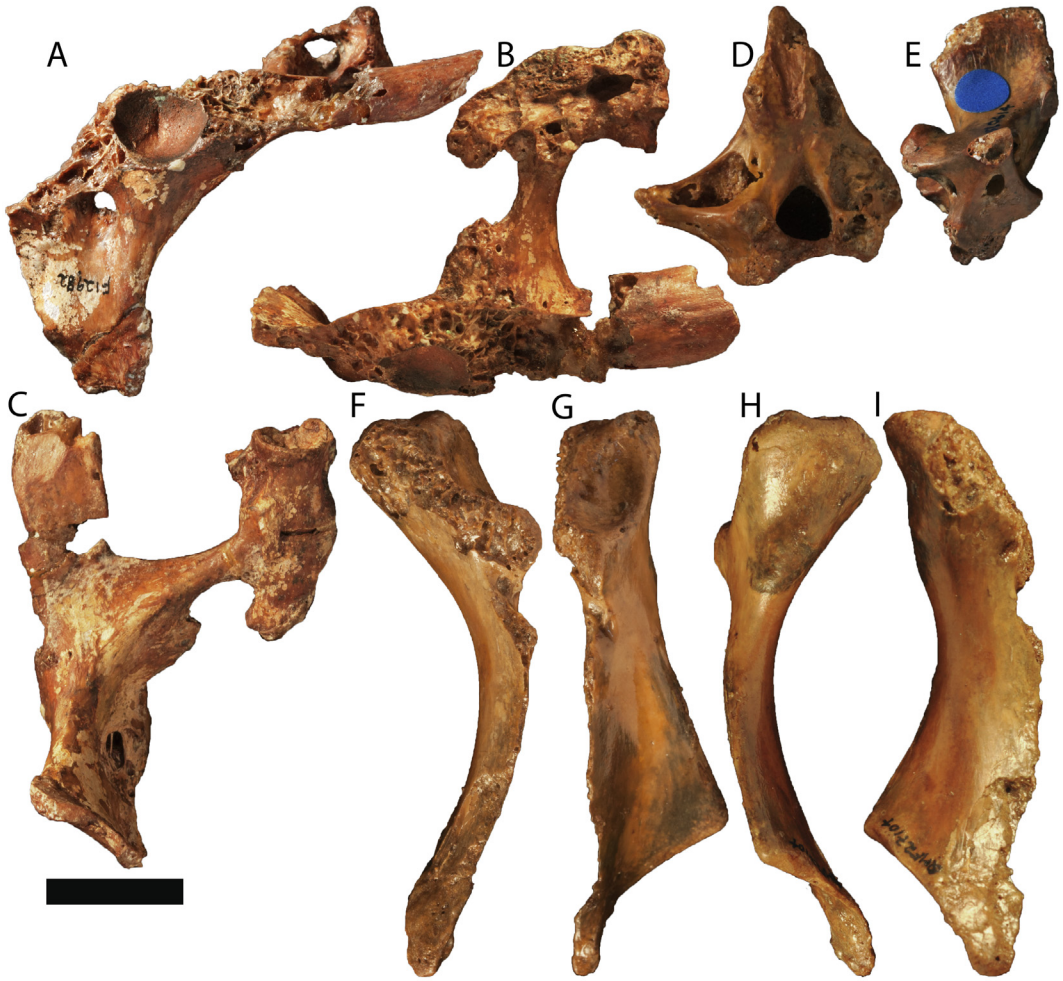

Fig. 3. Partial pterosaur pelvic material derived from the upper Albian Toolebuc Formation. **A–C,** partial right pelvis, QM F12982 in **A,** lateral, **B,** ventral and **C,** anterior views. **D–E,** presacral vertebra, QM F10614 in **D,** posterior and **E,** left lateral views. **F–I,** partial right pubis, QM F27104 in **F,** left lateral, **G,** anterior, **H,** right lateral and **I,** posterior views. All photographs taken by S.F.P. Scale bar equals 20 mm.

The vertebra (Fig. 3D–E) from the Toolebuc Formation (QM F10614) was initially described as a presacral vertebra (Molnar and Thulborn, 1980), and was interpreted as potentially the last dorsal vertebra of a large pterosaur (Kellner et al., 2010). Molnar (1987) noted that the form of the presacral vertebra suggested the presence of a notarium, a feature observed in pteranodontids, among other pterosaurs. Aside from the large pneumatic opening situated on the posterior surface of the transverse process, and a thick, anteroposteriorly elongated neural spine, QM F10614 possesses no other diagnostic features (Kellner et al., 2010). It seems likely QM F10614 represents an indeterminate ornithocheirid.

A partial pelvis discovered east of Boulia (Fig. 3A–C), comprising parts of the right ilium, right pubis, prepubis and right ischium (QM F12982, cast MN 4721-V), was regarded by Molnar (1987) as a perfect match in size to that of *Pteranodon* (YPM 1175) reconstructed by Eaton (1910, pl. XI). More recently, Hyder et al. (2014) illustrated QM F12982 alongside the pelves of ornithocheiroid pterodactyloids (page 115, figure 5). Furthermore, Molnar and Thulborn (2007), noted that the suture (=cleft) between the pubis and ischium in QM F12982 is less prominent when compared with that of *Anhanguera santanae*, whereas in *Pteranodon* both elements are completely fused. Given its incompleteness, it is not known whether QM F12982 possessed pubic plates fused along their ventral margin, as observed in *Pteranodon* and some ornithocheirids (Bennett, 1992, 2001; Veldmeijer, 2003a), or ventrally open pubic plates (Kellner and Tomida, 2000). Nor is it known whether the postacetabular process of QM F12982 was "hatchet-shaped", as in *Pteranodon* and in azhdarchoids, or if this process partially fused to the supraneural plate, an exclusive feature of *Pteranodon* (Bennett, 2001; Hyder et al., 2014). Sexual dimorphism has been noted in the pelves of *Pteranodon*, with puboischiadic plates deeper and more deeply emarginated in putative females (Bennett, 1992; Lü et al., 2011). The dorsal deflection of the preacetabular process, as well as a broad angle (greater than 90°) between the former and the anterior margin of the pubis confirms the assignment of QM F12982 to the Ornithocheiridae. It is uncertain whether sexual dimorphism affected the morphology of the puboischiadic plates in the Ornithocheiridae.

A partial pubis (QM F27104; Fig. 3F–I) derived from the Toolebuc Formation near Elizabeth Springs, near Boulia was figured but not described by Molnar and Thulborn (2007). It was assigned to the Ornithocheiridae, on the basis of a broad angle (considerably exceeding 90°) formed between the preacetabular process and anterior margin of the pubis (*sensu* Kellner, 2003a,b) aff. *Anhanguera*. Molnar and Thulborn (2007) regarded QM F12982 and a pubis (QM F27104) from the Toolebuc Formation as representative of the same taxon, on the basis of their overall similarity. In his analysis of *Rhamphorhynchus muensteri*, Bennett (1995) noted the position and length of the preacetabular process, postacetabular process and pubis changed during ontogenetic stages. Although it

is unlikely Ornithocheiridae experienced the same ontogenetic changes in the pelvis as observed in *Rhamphorhynchus*, ornithocheirids nevertheless show considerable variation in the morphology of the pubis (Hyder et al., 2014). Given that in some members the pubis and ischium fuse to form an expanded puboischiadic plate (Hyder et al., 2014), the morphology of the pubis in these members presumably did change significantly during ontogeny. Consequently, it cannot be assumed that the morphology of the pubis in subadult individuals would be near-identical to that of adults of the same species. Although QM F27104 and QM F12982 might belong to the same taxon, until more complete material becomes available this will remain uncertain.

The first pterosaur taxon named from Australia, *Mythunga camara* (QM F18896; Molnar and Thulborn, 2007), is known from a partial skull, consisting of the snout and part of the jaw (Fig. 2M–P), found embedded in a calcareous nodule from the upper Albian Toolebuc Formation near Hughenden, Queensland. The specimen was illustrated and described by Molnar and Thulborn (2007), who regarded QM F18896 as an archaeopterodactyloid (*sensu* Kellner et al., 2003). By contrast, Fletcher and Salisbury (2010) regarded *Mythunga camara* as an ornithocheirid, based on similarities between the morphology of the first tooth preserved in the upper jaw and the 12th and 13th tooth position in specimens referred to *Anhanguera*. In their original description, Molnar and Thulborn (2007) regarded QM F18896 as a short-snouted pterosaur, represented by "one-third to one-half of the skull and jaws" (p. 462). By contrast, Fletcher and Salisbury (2010) suggested the anterior-most portion of the *Mythunga* holotype skull is incomplete such that the preserved skull represents a fifth of the total skull length. Kellner et al. (2010) also suggested the specimen is incomplete near the rostral tip, preventing comparison with *Aussiedraco molnari*. As noted by Fletcher and Salisbury (2010), the size of the jaw and dentition therein is more consistent with the Ornithocheiridae (Kellner and Tomida, 2000; Kellner, 2003a,b; Unwin, 2001, 2003). Following a redescription and revised diagnosis, *Mythunga* was included in a phylogenetic analysis by Pentland and Poropat (2019) (modified based on the dataset of Andres et al. (2014)) and was subsequently recovered within Ornithocheiridae. Combined with observations of the holotype specimen by Pentland and Poropat (2019), as well as subsequent phylogenetic analyses (Pentland et al., 2019; Pentland et al., 2022a), these results demonstrate *Mythunga* is an unequivocal member of this clade. Interestingly, the inclusion of *Ferrodraco* in the Andres et al. (2014) had a stabilising effect on the position of *Mythunga* (Pentland and Poropat, 2019). To date, all phylogenetic analyses that have included both *Mythunga* and *Ferrodraco* have either resolved the two as sister taxa or in a polytomy with one or more additional taxa, demonstrating their close phylogenetic relationship (Holgado and Pêgas, 2020; Pentland et al., 2019; Pentland et al., 2022a). By contrast, *Aussiedraco* has not been resolved in a polytomy with, or as sister taxon to, either *Mythunga* or *Ferrodraco* (Holgado and Pêgas, 2020; Pentland et al., 2019; Pentland et al., 2022a).

A complete, right wing metacarpal (NMV P197962) derived from the Toolebuc Formation was discovered at Slashers Creek Station, east of Boulia, Queensland and described by Kellner et al. (2010). Although the specimen is complete, it has been severely anteroposteriorly crushed, with the exception of the distal articular surface, which has suffered comparatively little deformation. Based on comparisons with *Anhanguera piscator* (NSM-PV 19892) and AMNH 22552, Kellner et al. (2010) suggested it might have belonged to an individual with an estimated wingspan of 4 m. In their original description the authors concluded NMV P197962 shared more features with the Ornithocheiridae than other members of the Pteranodontoidea (Kellner and Tomida, 2000; Wellnhofer, 1985), based on the position of the pneumatic foramen. The interpretation of NMV P197962 as an ornithocheirid is supported here. As noted by Kellner et al. (2010), four small depressions located on the anterior surface likely represent tooth marks indicative of scavenging post-mortem and prior to fossilisation. NMV P197962 was recently figured by Pentland et al. (2022a), who noted that the proximodistal length and maximum width of the distal articular surface are greater than the metacarpal IV of *Ferrodraco* (based on the complete but anteroposteriorly flattened left metacarpal IV of that taxon).

A cervical vertebra (SAM P41968) derived from the upper Albian Toolebuc Formation was illustrated and described by Kellner et al. (2010). This specimen is incomplete dorsally, lacking most of its neural arch and displaying oblique shearing across the zygapophyses; consequently, the true height of the neural spine cannot be determined. Nevertheless, the length/width ratio < 2.5 excludes SAM P41968 from both Azhdarchidae and Archaeopterodactyloidea (Kellner et al., 2010). The similar morphologies of cervical vertebrae 3–7 in Ornithocheiridae and *Pteranodon* mean that the serial position and taxonomic affinities of SAM P41968 are difficult to determine (Kellner et al., 2010). Kellner et al. (2010) regarded SAM P41968 as a probable ornithocheirid, based on the presence of postexapophyses and strongly developed lateral pneumatic foramina; they also concluded that SAM P41968 represents a mid-cervical vertebra.

A partial mandibular rostrum (QM F44423; Fig. 2Q–T) recovered from east of Hughenden, equivalent in age to the upper Albian Toolebuc Formation, was illustrated and described by Fletcher and Salisbury (2010) as an indeterminate ornithocheirid. Although the rostrum possesses no *in situ* teeth, a partial crown was recovered in close proximity to the specimen, and was interpreted by the authors as a tooth belonging to the mandible, with its original position indeterminate (Fletcher and Salisbury, 2010). As noted by Fletcher and Salisbury (2010), QM F44423 preserves alveoli 1–8 on the left ramus, and 1–7 on the right. Unfortunately, due to the presence of matrix on the rostral-most end of the mandible, some features are obscured, with the authors tentatively suggesting the mandible may possess an additional pair of teeth rostral to those figured. As noted by Kellner et al. (2011) QM F44423 differs from *Aussiedraco*, in that it has a straight dorsal surface and curved ventral margins. Until more complete material becomes available, QM F44423 is regarded here as an indeterminate ornithocheirid, following Fletcher and Salisbury (2010). QM F44423 differs from other members of the Ornithocheiridae in that there seems to be little variation in tooth size along the tooth row (Fletcher and Salisbury, 2010; Tab. 1). The specimen also lacks the terminal expansion of the mandible and mandibular crest observed in *Tropeognathus* and *Anhanguera*. As stated by Fletcher and Salisbury (2010), mandibular crests are absent in several ornithocheirids, including *Brasileodactylus* (MN 4804-V), *Boreopterus* (JZMP – 04–07 – 3) and *Ludodactylus sibbicki* (SMNK PAL 3828), which might be attributable to sexual dimorphism. Fletcher and Salisbury (2010) also noted a personal communication with David Unwin wherein he suggested anterior expansion of the mandible and tooth size are proportionate and related to size and ontogeny. Although there are distinct morphological features that distinguish QM F44423 from *Aussiedraco*, Pêgas et al. (2019) regarded QM F44423 as most similar to *Aussiedraco* and *Targaryendraco* than any other pterosaur material. The fact that the alveolar borders are raised in QM F44423 (such that the jawline is scalloped) differentiates it from members of the Boreopteridae and Lonchodraconidae, as well as *Ornithocheirus simus* (Pêgas et al., 2019). As noted by Pentland et al. (2022a), QM F44423 clearly differs from *Ferrodraco* because the latter possesses the remnants of a mandibular crest, and although the first tooth pair in both specimens is oriented vertically, they differ in other aspects of their dentition. Based on comparisons with other members of the

Tropeognathinae, it seems unlikely that QM F44423 belongs within this clade. However, given that the ontogenetic status of QM F44423 cannot be determined in the absence of more complete material, it would be premature to rule out the possibility that this specimen is an immature individual.

The proximal end of a left metacarpal IV (QM F44321; Fig. 2U–Y) was recovered from the upper Albian Toolebuc Formation, northeast of Boulia (Fletcher and Salisbury, 2010). QM F44321 was assigned to cf. *Anhanguera* by Fletcher and Salisbury (2010), on the basis that it was most similar to metacarpals known from this genus. Fletcher and Salisbury (2010) noted that the morphology of QM F44321, specifically the tuberculum and associated sulcus is distinct from any described species. As noted by Fletcher and Salisbury (2010), the morphology of the proximal articular surface of metacarpal IV can vary widely among ornithocheirids (see Fletcher and Salisbury, 2010: fig. 5). Differences in the morphology of the proximal articular surface might be indicative variation in the degree of rotation between the carpal elements (i.e. the distal syncarpals) and the wing metacarpal (Pentland et al., 2022a). Although it is likely that QM F44321 can be referred to the Ornithocheiridae, it cannot be determined whether it belongs to *Mythunga, Aussiedraco, Thapunngaka,* or represents a separate taxon.

The distal portion of a wing phalanx (QM F44312; Fig. 2Z–AD) was recovered from the upper Albian Toolebuc Formation on Dunluce Station, Hughenden and described by Fletcher and Salisbury (2010). QM F44312 was regarded as an ornithocheirid cf. *Anhanguera*, as the morphology of the shaft in cross section and distal articular head are similar to that of '*Santanadactylus pricei*' (BSP 1980 I 122) (Fletcher and Salisbury, 2010). However, '*Santanadactylus pricei*' is considered by some pterosaur workers as non-diagnostic, and an indeterminate pterodactyloid (Barrett et al., 2008; Kellner and Tomida, 2000). Fletcher and Salisbury (2010) regarded QM F44312 as either wing phalanx I or wing phalanx II, but did not specify whether QM F44312 was a left or right. As noted by Pentland et al. (2022a), QM F44312 appears to be from the left, based on comparisons with '*Santanadactylus pricei*' (Wellnhofer, 1991a). In the absence of any diagnostic features, QM F44312 is considered here Pterodactyloidea indet.

The second Australian pterosaur taxon to be named, *Aussiedraco molnari* (QM F10613; Fig. 2D–G), was established on the basis of a mandibular symphysis that was initially considered to be from a species closely related to *Ornithocheirus* Seeley, 1869 (Molnar and Thulborn, 1980). Unwin (2001) assigned this specimen to *Anhanguera*? *cuvieri*, a species which has been assigned to the genus *Cimoliopterus*, a pteranodontoid of indeterminate affinities (Rodrigues and Kellner, 2013). QM F10613 was then referred to aff. *Lonchodectes* by Molnar and Thulborn (2007), and later to aff. *Ornithocheirus* by Myers (2010). Kellner et al. (2011) concluded that *Aussiedraco* could not be referred to *Ornithocheirus*, nor to *Lonchodectes* or *Anhanguera*; instead, they suggested that it represented a new taxon, *Aussiedraco molnari*, based on the shape of the mandibular symphysis, its dentition, and absence of a dentary crest. On the basis of a narrow midline groove, as well as the size and shape of the alveoli, Kellner et al. (2011) assigned *Aussiedraco molnari* to the Pteranodontoidea, in a more derived position relative to the Istiodactyliformes, Ornithocheiridae and *Pteranodon* (and other related taxa). In their original description of the specimen, Molnar and Thulborn (1980) observed that the fourth alveolus is occupied by a small and incompletely erupted tooth. The tooth does not fill the alveolus, and was interpreted by the authors as a replacement stage after the loss of the previous functional tooth (Edmund, 1960). The replacement tooth has a thin, labiolingually compressed crown (Molnar and Thulborn, 1980). As noted by Kellner et al. (2011), the shape of the alveoli and morphology of the unerupted tooth excludes QM F10613 from Istiodactyliformes, which characteristically possess triangular, strongly labially compressed teeth (Andres and Qiang, 2006; Howse et al., 2001; Wang et al., 2008). More recently, *Aussiedraco* was included in a phylogenetic analysis by Pêgas et al. (2019) and resolved as a member of a new clade, the Targaryendraconia, comprising *Targaryendraco*, *Aussiedraco*, *Barbosania*, *Aetodactylus*, *Camposipterus* and *Cimoliopterus*. As noted by Pêgas et al. (2019) the width of the mandible in *Aussiedraco* is consistent along its anteroposterior length, with the exception of the transversely wider third mandibular tooth pair. The third tooth pair of the mandible are also laterally expanded relative to the lateral margins of the jaw (Pêgas et al., 2019). *Aussiedraco* and *Targaryendraco* are similar in that the mandibular groove extends to the anterior tip of the mandible (Pêgas et al., 2019); however, the latter bears an odontoid process, a feature absent in *Aussiedraco*. Pêgas et al. (2019) regarded an enlarged first tooth pair of the mandible as a defining characteristic of the targaryendraconids; however, the mesiodistal length of the first and second tooth pair on the left in *Aussiedraco* are exactly the same (8.3 mm, pers. observ.). Although the right first tooth pair is enlarged relative to the second tooth pair (6.7 mm and 4.4 mm, respectively) it is worth noting that the second tooth pair on the right is incomplete as a result of erosion or over-preparation. Nevertheless, the fact that there is no difference in the mesiodistal lengths of the first and second alveoli on the better preserved surface of the *Aussiedraco* type specimen casts doubts on the validity of this character as a defining feature of this clade. Interestingly, two sulci are preserved on the occlusal surface of the rostral tip of the mandible in *Aussiedraco*, a feature not known from any other pterosaur. Although this feature might represent an autapomorphy, it is also possible that the *Aussiedraco* holotype was over-prepared (chemically with acetic acid). If this conjecture is correct, perhaps the two sulci might in fact represent the remnants of a bifurcating mandibular groove. A bifurcating tip of a mandibular groove was also observed in *Cearadactylus atrox* by Vila Nova et al. (2014); however unlike *Aussiedraco* the dentary is laterally expanded in *Cearadactylus*.

Putative pterosaurian remains have also been recovered from the Hazel Creek assemblage from the upper Albian Toolebuc Formation (Traub et al., 2017). It is not known whether the material comprises identifiable elements or is diagnostic. Further work is required to determine the pterosaurian affinities of the Hazel Creek material and, until such time, they are considered only putative pterosaur remains.

More recently, *Thapunngaka shawi* was described based on a partial mandible (KK F494) from the Toolebuc Formation near Richmond by Richards et al. (2021). *Thapunngaka* differs from *Tropeognathus mesembrinus*, in that the former possesses a larger mandibular crest, which differs in shape when observed in lateral view (Richards et al., 2021). Phylogenetic analysis recovered *Thapunngaka* in a polytomy with two other Australian pterosaur taxa, *Mythunga* and *Ferrodraco*, suggesting a radiation of Early Cretaceous pterosaurs within the Eromanga Basin (Richards et al., 2021). This clade was resolved as sister to *Tropeognathus mesembrinus* + *Siroccopteryx moroccensis* (Richards et al., 2021).

A partial ornithocheirid femur (NMV P231549) from the upper Albian Toolebuc Formation on Slashers Creek Station, Boulia was described and figured by Pentland et al. (2022b). This specimen is three-dimensionally preserved and comprises the proximal articular surface and part of the shaft, with internal trabeculae visible in distal view (Pentland et al., 2022b). The morphology of NMV P231549 is similar to that of *Anhanguera piscator*, in that both specimens demonstrate a similar deflection of the femoral head, relative to the diaphysis (Pentland et al., 2022b).

8.3. Griman Creek Formation

Smith and Smith (1999) figured two possible pterosaur limb bones from the Lower Cretaceous (mid-Cenomanian) Griman Creek Formation at Lightning Ridge in northern New South Wales; however, these specimens await formal description, and their whereabouts are currently unknown. Recently, two isolated teeth (LRF 759 and LRF 3142) preserved as natural casts in non-precious opal from the Griman Creek Formation were described by Brougham et al. (2017) and identified as pterosaurian, belonging to indeterminate members of the Ornithocheiridae. Both specimens are oval in cross-section, labiolingually compressed and slightly lingually recurved, and similar in length to the dentition of *Mythunga camara* (Brougham et al., 2017). The presence of fine, longitudinal striations on LRF 759 suggests affinities with the Ornithocheiridae; however, teeth belonging to some members of this group are smooth.

8.4. Mackunda Formation

The proximal end of a left pterosaur humerus (QM F42739; Fig. 2H–L) was discovered at Vellum Downs, approximately 100 km southwest of Hughenden in the upper half of the upper Albian Mackunda Formation. QM F42739 comprises a 75 mm fragment of a long bone which was tentatively identified by Fletcher and Salisbury (2010) as an indeterminate ctenochasmatoid. If correct, QM F42739 represents the first ctenochasmatoid from Australia (Fletcher and Salisbury, 2010), and one of only two non-ornithocheiroid pterosaur records from the continent. Unfortunately, damage to the proximal end prevents description of the ulnar crest; however, the articular surface is intact. QM F42739 lacks a proximally located pneumatic foramen, a feature characteristic of the Dsungaripteroidea (Kellner et al., 2004). As noted by the authors, QM F42739 does not belong to the Ornithocheiridae, as it lacks the warped deltopectoral crest of the Pteranodontoidea (Bennett, 1989) and instead possess a 'crescent-shaped' crest. Fletcher and Salisbury (2010) also noted similarities between QM F42739 and MOZ 3625P, regarded as medium-sized pterodactyloid from Tithonian Vaca Muerta Formation in the Neuquén Basin, northwest Patagonia.

8.5. Winton Formation

Ferrodraco lentoni (AODF 876), the third Australian pterosaur taxon to be named, was established based on the most complete pterosaur skeleton ever reported from Australia (Pentland et al., 2019). The holotype specimen was found in April 2017 on Belmont Station, northeast of Winton, and derives from the Cenomanian–lowermost Turonian Winton Formation (Pentland et al., 2022a). The *Ferrodraco lentoni* holotype preserves a partial skull, which comprises part of the premaxillary crest, premaxilla, maxilla and mandibular symphysis, as well as the left frontal and left mandibular articular region (Pentland et al., 2019). Preserved axial elements include five incomplete cervical vertebrae, whereas the appendicular skeleton includes elements from both wings (Pentland et al., 2019). Only two appendicular elements are from the right side: a partial scapulocoracoid, and the proximal end of metacarpal IV (Pentland et al., 2019). The left wing is represented by the distal ends of the left ulna and radius, an almost complete syncarpus, metacarpal IV (complete but anteroposteriorly flattened), the proximal end of the first wing phalanx, a partial non-wing metacarpal, and partial non-wing manual phalanges (Pentland et al., 2022a). The specimen is three-dimensionally preserved, and fusion of the scapulocoracoid, as well as the extensor tendon process to the first wing phalanx indicates this individual was osteologically mature (Pentland et al., 2019). Moreover, the specimen was semi-articulated during fossilisation, based on key-fits between ironstone matrix attached to anatomically adjacent elements (Pentland et al., 2019). The phylogenetic position of *Ferrodraco* was first assessed by Pentland et al. (2019) who utilised modified datasets of Andres et al. (2014) and Lü et al. (2018). The phylogenetic analysis based on the dataset and methods of Andres et al. (2014) resolved *Ferrodraco* occupying the most derived position within Ornithocheiridae (Pentland et al., 2019). More recently, *Ferrodraco* has been resolved as a member of the Tropeognathinae, a clade comprising *Ferrodraco* + *Mythunga*, with *Tropeognathus mesembrinus* + *Siroccopteryx moroccensis* resolved as the sister taxon to this clade (Holgado and Pêgas, 2020). It should be noted that Holgado and Pêgas (2020) only scored *Ferrodraco* for cranial and dental characters (despite Pentland et al. (2019) figuring the cervical vertebrae and the majority of the appendicular elements). A revised version of the Holgado and Pêgas (2020) dataset was presented by Pentland et al. (2022a) in which scores for *Mythunga, Aussiedraco* and *Ferrodraco* were updated. Despite these revisions, analysis of the Holgado and Pêgas (2020) dataset returned *Ferrodraco* and *Mythunga* as sister taxa (Pentland et al., 2022a). By contrast, using a revised version of the dataset presented by Pêgas et al. (2019), *Ferrodraco*, *Mythunga* and *Tropeognathus* formed a polytomy (Pentland et al., 2022a). Although their position within Ornithocheiridae remains somewhat uncertain, it is evident that *Ferrodraco* and *Mythunga* are closely related, and as noted by Holgado and Pêgas (2020), together they form a clade. Interestingly, members of the Tropeognathinae are so far restricted to Gondwana, comparing favourably with the Gondwanan provincialism of other terrestrial vertebrate clades from the Early Cretaceous (Agnolin et al., 2010; Herne et al., 2010; Novas et al., 2013; Smith et al., 2008).

A partial left pterosaur femur (AODF 2297) from the Cenomanian–lowermost Turonian Winton Formation was discovered during excavations made by the Australian Age of Dinosaurs in 2005 at the "Elliot site" (AODL 127) on Belmont Station, Queensland, Australia (Pentland et al., 2022b). The specimen was alluded to by Hocknull et al. (2009), and illustrated in a popular publication (Hocknull and Cook, 2007). AODF 2297 is three-dimensionally preserved, but incomplete, such that the femoral head, distal articular surface and an unknown portion of the distal end of the shaft are absent (Pentland et al., 2022b). Based on its gross morphology, AODF 2297 compares favourably with *Anhanguera piscator* (Kellner and Tomida, 2000); however, the lesser trochanter is more developed in the former (Pentland et al., 2022b). The greater trochanter of this specimen also preserves two circular indentations which were tentatively identified as bite marks inflicted by a crocodyliform (Pentland et al., 2022b).

8.6. Molecap Greensand

An incomplete jaw fragment (WAM 68.5.11) from the Molecap Hill quarry (uppermost Albian–Coniacian Molecap Greensand) near Gingin, Western Australia was described by Kear et al. (2010). As noted by Kear et al. (2010), raised alveolar borders suggests referral to the Pterodactyloidea. Moreover, as the alveolar spacing is greater than the alveolar diameter, WAM 68.5.11 cannot be referred to the Archaeopterodactyloidea or Istiodactyliformes (Kear et al., 2010). The jaw fragment with anterolaterally oriented alveoli compressed labiolingually, wide spacing and variable size seems consistent with the predominantly Early Cretaceous and geographically widespread Ornithocheiridae (Kear et al., 2010). Kear et al. (2010) tentatively assigned WAM 68.5.11 to the Ornithocheiridae. Given its general morphology, and the referral of other Australian pterosaurs to the Ornithocheiridae, the interpretation of WAM 68.5.11 as an ornithocheirid is tentatively supported here. Due to its fragmentary nature, it cannot be

determined whether WAM 68.5.11 represents an upper or lower jaw (Kear et al., 2010).

8.7. Miria Formation

The only pterosaur specimen known from the upper Maastrichtian Miria Formation is the proximal end of a right ulna (WAM 60.57), found in the Giralia Range, Western Australia (Bennett and Long, 1991). This was tentatively interpreted by Bennett and Long (1991) as an azhdarchid, comparable to *Arambourgiania* from Jordan (NHMUK PV R9228) on the basis of size similarities, relatively small biceps tubercle and pneumatic foramina on the anterior margin and located distal to the condyles. The authors noted that WAM 60.57 differs from the Dsungaripteridae in that the condyles are deflected posteriorly, rather than anteriorly. Based on comparisons with the Ornithocheiroidea, Bennett and Long (1991) suggested a minimum wingspan of 3.6 m and a maximum wingspan of 4.9 m. Given that the largest members of the Dsungaripteroidea are reported to have had wingspans of 3 m, referral of WAM 60.57 to this clade seems unlikely. According to Bennett and Long (1991) the ulna may represent a pterosaur more closely related to the Azhdarchidae, as neither tapejarids nor dsungaripterids are recorded in Maastrichtian deposits thus far. This conclusion has also been supported by Kellner et al. (2010). WAM 60.57 differs from that of *Azhdarcho lancicollis*, CCMGE 1/11915, (previously designated TsNIGRI, LU-N 1/11915) in possessing a more developed medial condyle and larger dorsal articular surface. Comparisons between WAM 60.57 and *Montanazhdarcho minor* (MOR 691) are limited as the latter is crushed proximally, resulting in distortion of the proximal end. By contrast, WAM 60.57 is dorsoventrally elongate when compared with *Quetzalcoatlus northropi* (Andres and Langston Jr, 2021). Moreover, the ventral expansion is more pronounced and the dorsal cotyle anteroposteriorly expanded in *Quetzalcoatlus*, when compared with WAM 60.57 (Andres and Langston Jr, 2021). We suggest that Upchurch et al. (2015) erred in stating that WAM 60.57 was an indeterminate pterodactyloid from the Campanian, when it is in fact a Maastrichtian azhdarchid (Upchurch et al., 2015, Tab. 1).

9. New Zealand

9.1. Maungataniwha sandstone member, tahora formation

The first pterosaur fossil described from New Zealand was the distal end of a left ulna (CD 467) of an indeterminate pterodactyloid collected from the Upper Cretaceous (upper Campanian–lower Maastrichtian) Maungataniwha Sandstone Member of North Island (Molnar and Wiffen, 1994; Wiffen and Molnar, 1988). Wiffen and Molnar (1988) compared the partial ulna with pterosaur ulnae from elsewhere and noted that it was most similar to '*Anhanguera araripensis*' and *Dsungaripterus weii*. Alongside the ulna, near the crushed end of the shaft, lodged in the sandstone matrix was a strongly curved tooth, split across its longitudinal axis (Wiffen and Molnar, 1988; Fig. 1D). On the basis of its proximity to the ulna, Wiffen and Molnar (1988) suggested it was most likely derived from the same individual and compared the tooth morphology to that of '*Santanadactylus araripensis*' (Wellnhofer, 1985). If the partial ulna and tooth did belong to the same individual, CD 467 cannot be a dsungaripterid as it possesses lingually curved teeth and is tentatively suggested here as more similar to *Anhanguera araripensis*. However, it is also possible that the tooth does not belong to a pterosaur and may in fact belong to a plesiosaur.

The second pterosaur reported from New Zealand was a purported pterosaur scapula (GNS CD 547; Molnar and Wiffen, 1994). GNS CD 547 was originally identified as pertaining to an indeterminate azhdarchid, but was later reinterpreted as a fragmented coracoid by Averianov (2014a), who regarded both the ulna (CD 467) and coracoid as indeterminate members of the Azhdarchidae.

More recently, the partial left ulna (CD 467) recovered from the Maungataniwha Sandstone Member has been interpreted as a lonchodectid (Albuquerque, 2019); however, this designation is highly problematic. Although the pre-print was made available in December 2019, given that this publication has not been peer-reviewed, this ulna is regarded here as an indeterminate azhdarchid.

10. Antarctica

10.1. Hanson Formation, Antarctica

A pterosaur humerus (FMNH PR 3052) was reported from the Lower Jurassic Central Transantarctic Mountains by Hammer and Hickerson (1994) and was tentatively identified as a medium-sized dimorphodontid (Hammer and Hickerson, 1996). FMNH PR 3052 was figured by Hammer and Hickerson (1999) but awaits formal description. This specimen was collected on Mt. Kirkpatrick (Beardmore Glacier region, Transantarctic Mountains), and interpreted as Sinemurian–Pliensbachian in age (Hammer and Hickerson, 1996). Although early reports indicate this material was collected from the Falla Formation (Hammer and Hickerson, 1996; Hammer and Hickerson, 1994) their provenance was later given as the Hanson Formation (Hammer and Hickerson, 1999), concordant with associated field data of FMNH PR 3052 (W. Simpson, pers. comm). The specimen was regarded as an indeterminate member of the Rhamphorhynchoidea by Barrett et al. (2008). When summarising pterosaurian palaeobiogeography, Upchurch et al. (2015) erred stating the humerus was from the Cretaceous (Maastrichtian) (Upchurch et al., 2015, Tab. 1).

10.2. Santa Marta Formation, Antarctica

More recently, Kellner et al. (2019b) described and figured two isolated pterodactyloid pterosaur specimens from the Cretaceous of Antarctica, including the distal end of a first wing phalanx (MN 7800-V), collected from a moraine (Santonian–lower Campanian Lachman Crags Member of the Santa Marta Formation) at Abernathy Flats on James Ross Island. Until perinatal and/or very young pterosaur remains are collected from Antarctica, it remains uncertain as to whether these high latitude pterosaurs were in fact nonmigratory year-round residents.

10.3. Snow Hill Island Formation, Antarctica

Kellner et al. (2019b) described and figured a second specimen from the Cretaceous of Antarctica: a wing metacarpal IV (MN 7801-V) from the Maastrichtian Snow Hill Island Formation on Vega Island. Unfortunately, MN 7801-V sustained subsequent damage as a result of the fire that devastated the Museu Nacional (Kellner, 2019). The authors suggest that MN 7800-V might have belonged to an individual with an estimated wingspan of 3–4 m, based on comparisons with *Anhanguera piscator* (Kellner and Tomida, 2000). MN 7801-V is suggested to have belonged to a slightly larger individual, with an estimated wingspan of 4–5 m based on comparisons with AMNH 22555 and AMNH 22552 (Wellnhofer, 1991a), *Anhanguera piscator* (Kellner and Tomida, 2000), *Pteranodon* (Bennett, 2001), and other pterodactyloids (Kellner, 2003a,b; Wellnhofer, 1991b). Both MN specimens demonstrate that large pterodactyloids were present at high latitudes during the Cretaceous (Fig. 4), with MN 7801-V indicating that

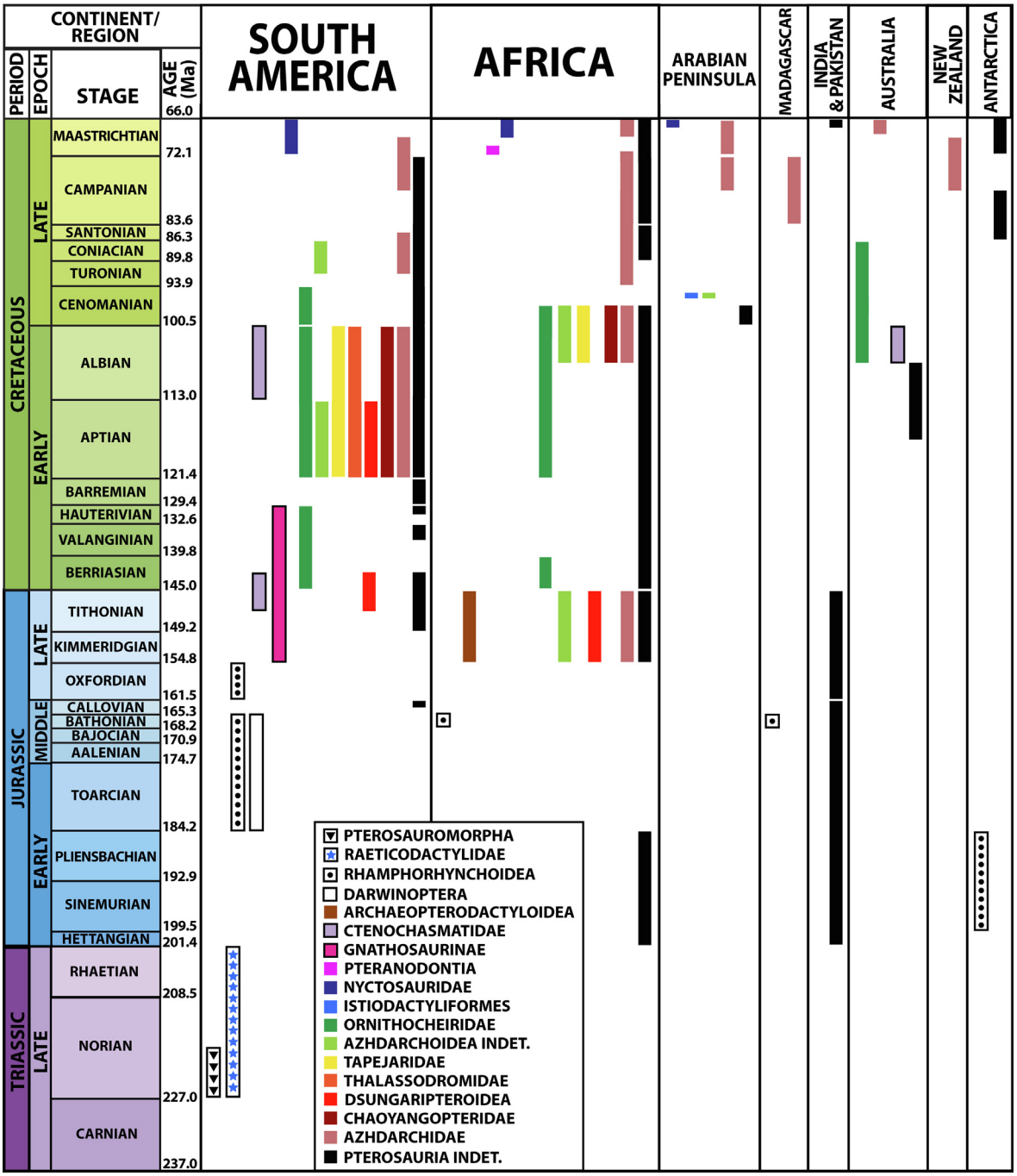

Fig. 4. Chart of Gondwanan pterosaur diversity through time. Timespans indicated for each clade indicates the maximum range of possible ages that can be applied to the stratigraphic unit(s) from which it derives, rather than its strict temporal distribution. Timespans are not indicative of taxonomic diversity or relative abundance.

pterodactyloids were present in Antarctica until the Maastrichtian (Kellner et al., 2019b).

11. Discussion

As noted by Upchurch et al. (2015) the pterosaur fossil record is patchy, both temporally and geographically. As such, comparisons between the Gondwanan and Laurasian pterosaur palaeobiogeography are provisional. Nevertheless, despite the description of new material, and revision of holotype specimens, the origins and biogeographical history of the Pterosauria remains controversial (Andres, 2012; Baron, 2021; Unwin, 1996). At present, the earliest definitive pterosaurs are Norian in age, with non-pterodactyloid pterosaurs predominantly known from the Northern Hemisphere (see Martínez et al., 2022 and references therein). Aside from specimens from the Triassic of Italy (Dalla Vecchia, 2013), there are comparatively few non-pterodactyloid pterosaurs from Triassic strata in Gondwana. Recent analysis has classified two of the non-pterodactyloids from South America outside Pterosauria: the *Faxinalipterus* holotype (UFRGS PV0927T) is resolved within Lagerpetidae, whereas the previously referred specimen (UFRGS PV0769T) is now considered a pterosauromorph (*sensu* Ezcurra et al., 2020) and holotype of *Maehary bonapartei* (Kellner et al., 2022). Despite this, the recently described *Yelaphomte praderioi* (PVSJ 914) and *Pachagnathus benitoi* (PVSJ 1080) from the Late

Triassic of Argentina demonstrate the presence of raeticodactylids in Gondwana (Martínez et al., 2022). Unfortunately, ascertaining the distribution of other non-pterodactyloid clades in Gondwana is much more difficult, as many are incomplete and thus have uncertain affinities. A lack of anatomical overlap between the '*Campylognathoides indicus*' holotype and referred specimens necessitates reappraisal of the postcranial remains pertaining to this taxon (Codorniú and Gasparini, 2012; Padian, 2008b). Moreover, given that the pterosaurian affinities of the cranial material attributed to '*Campylognathoides indicus*' have been questioned by Padian (2008b), reassessment of the holotype specimen is required to determine the validity of this taxon. The remaining non-pterodactyloid specimens from Gondwana include the darwinopteran *Allkaruen koi* (Codorniú et al., 2016a), isolated rhamphorhynchid teeth from the Bathonian of Madagascar (Dal Sasso and Pasini, 2003), and an isolated humerus from the Jurassic of Antarctica (FMNH PR 3052; Hammer and Hickerson, 1996). Although initially interpreted as a medium-sized dimorphodontid by Hammer and Hickerson (1996), FMNH PR 3052 was more recently regarded as an indeterminate rhamphorhynchoid by Barrett et al. (2008). Given that very few pterosaurs are known from the Early Jurassic of Gondwana, the specimen has important implications for pterosaur evolution. Irrespective of the taxonomic status of FMNH PR 3052, rhamphorhynchids were present in the Triassic ecosystems of Gondwana (Dal Sasso and Pasini, 2003). By contrast, anurognathids are known exclusively from Eurasia (Cheng et al., 2016; Hone, 2020; Wang et al., 2010).

The Gondwanan pterosaur assemblage largely comprises pterodactyloids, with most major clades represented (Fig. 4). The presence of ctenochasmatids in the Late Jurassic and Early Cretaceous of Africa and South America closely matches the temporal distribution of Laurasia (Witton, 2013). Moreover, the presence of gnathosaurines in the Upper Jurassic of Uruguay (Perea et al., 2018; Soto et al., 2021) lends support to the hypothesis that ctenochasmatids might have spread from Eurasia to South America via the Hispanic corridor, as suggested by Martill et al. (2006).

Ornithocheiridae has been reported from the Early Cretaceous of South America, Africa, Australia and the Arabian Peninsula (Fig. 4). We suggest that their apparent absence from the remaining Gondwanan continents is a consequence of undersampling, and that this clade was cosmopolitan during the Early Cretaceous. The stratigraphic distribution of ornithocheirids from Gondwana closes matches that of Laurasia (Barrett et al., 2008; Upchurch et al., 2015; Witton, 2013).

In Laurasia, pteranodontians are known from the Late Cretaceous; whereas, in Gondwana, this lineage is solely represented by *Epapatelo otyikokolo* from the Maastrichtian Mocuio Formation of Angola (Fernandes et al., 2022). Although Laurasian pteranodontians are known from slightly older stratigraphic horizons, notably the Coniacian to Campanian of North America (see Kellner, 2010 and references therein) and the upper Campanian of Russia (Averianov and Kurin, 2022; Bogolyubov, 1914), this clade likely achieved a cosmopolitan distribution by the Maastrichtian.

Tapejarids are known exclusively from the Early Cretaceous of Laurasia (Lü et al., 2006a; Lü et al., 2006b; Lü et al., 2007; Martill et al., 2020a; Vullo et al., 2012; Wang and Zhou, 2003b; Zhang et al., 2019), and the Early Cretaceous of Gondwana (Frey et al., 2003b; Kellner, 1989, 2013; Kellner and Campos, 2007b; Martill et al., 2020b; Pêgas et al., 2016; Unwin and Martill, 2007; Wellnhofer and Buffetaut, 1999b; Campos and Kellner, 1997; Kellner et al., 1994; Kellner et al., 2002; Kellner et al., 2013). Given the prevalence of this clade during the Aptian–Albian, future excavations in penecontemporaneous horizons will likely result in additional tapejarids, and potentially new taxa.

Gondwanan dsungaripteroids are predominantly known from the Early Cretaceous of South America and include *Domeykodactylus ceciliae* (Martill et al., 2000) and *Puntanipterus globosus* (Bertozzo et al., 2021; Galton, 1980; Ji, 2020; Lü et al., 2009; Wellnhofer, 1991b). Although *'Santanadactylus spixi'* has also been referred to this clade (Bennett, 1989; Lü et al., 2009), other workers regard it as a tapejarid (Averianov et al., 2005; Kellner, 1995). Outside of South America, the only other Gondwanan dsungaripteroids are *Tendaguripterus* (Unwin and Heinrich, 1999) and a partial humerus MB.R.2828, both reported from the Tendaguru Formation of Tanzania, Africa (Costa and Kellner, 2009). The stratigraphic distribution of the dsungaripteroids from Gondwana compares favourably with that of Laurasia (Upchurch et al., 2015; Witton, 2013). As with the hypothesised dispersal of the ctenochasmatids (Martill et al., 2006), it is possible that the dsungaripteroids might have dispersed from Eurasia to South America via the Hispanic corridor.

The Chaoyangopteridae are predominantly known from the Early Cretaceous of China (Dong et al., 2003; Lü and Ji, 2005; Lü and Zhang, 2005; Lü et al., 2008; Wang and Zhou, 2003a). At present, the only Gondwanan chaoyangopterid is *Apatorhamphus gyrostega*, which was first tentatively referred to the Chaoyangopteridae by McPhee et al. (2020). The taxonomic affinities of this specimen are supported by the recent phylogenetic analysis of Andres (2021). However, it remains contentious as to whether other chaoyangopterids were present in Cretaceous Gondwanan ecosystems. Previous phylogenetic analyses have resolved *Lacusovagus* within Chaoyangopteridae (Cerqueira et al., 2021; Leal et al., 2017), or alternatively, within the genus *Tupuxuara* (Wu et al., 2017). A more recent phylogenetic analysis resolves *Lacusovagus* within Tapejaridae (Andres, 2021). Similarly, *Microtuban* from the Late Cretaceous of Lebanon may represent either a thalassodromid or chaoyangopterid (Elgin and Frey, 2011b). Alternatively, a more recent phylogenetic analysis has resolved *Microtuban* outside of the Dsungaripteridae (Andres, 2021). McPhee et al. (2020) recently assigned *Banguela oberlii* to the Chaoyangopteridae; however, the latter has previously been regarded as a referred specimen of *Thalassodromeus sethi* (Pêgas et al., 2018).

As noted by Averianov (2014b) and demonstrated through this review, the Azhdarchidae are among the most prevalent pterosaur clade during the Late Cretaceous. Although their remains have not yet been reported from Indo-Pakistan and Antarctica (Fig. 4), this is most likely because of undersampling and undiagnostic material, and future excavations will likely result in the discovery of azhdarchids from every continent. Similarly, the apparent disparity in azhdarchid diversity between Laurasia and Gondwana is likely the result of temporal and geographic gaps, rather than habitat preference (see Averianov, 2014).

12. Conclusion

In spite of the patchy nature of the Gondwanan pterosaur record, particularly that of East Gondwana, the present review provides a comprehensive summary of Gondwanan pterosaurs. The identification of additional specimens, particularly from landmasses depauperate in pterosaur material, like Australia, Antarctica, New Zealand, India and Madagascar, may elucidate Gondwanan pterosaur palaeobiogeography. Although there is certainly potential for further work, it is hoped that the summary provided here will serve as a solid foundation for more detailed studies and future research.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank the Paleobiology Database for ensuring and maintaining records summarising fossil occurrences from scientific publications is made publically available. A.H.P.'s work on this project was funded by Swinburne University of Technology, through receiving a Student Emergency Fund Grant. A.H.P. and S.F.P. would like to thank: the Paleontological Society for an Arthur James Boucot Research Grant, which enabled firsthand observations of specimens at Queensland Museum; S. Hocknull, A. Rozefelds and K. Spring (Queensland Museum) for allowing A. H.P. and S.F.P. access to the Australian pterosaur specimens in their care; Tim Ziegler (NMV) facilitated collections access; Trish Sloan (AOD) provided collections access; P. Vickers-Rich, I. Somerville, D. Unwin, Roy Smith, Vahe Demirjian and an anonymous reviewer for helpful insights and reviews which greatly improved the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gr.2023.03.005.

References

Agnolin, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2010. A reappraisal of the Cretaceous non-avian dinosaur faunas from Australia and New Zealand: evidence for their Gondwanan affinities. J. Syst. Palaeontol. 8 (2), 257–300.

Aires, A.S., Kellner, A.W., Müller, R.T., Da Silva, L.R., Pacheco, C.P., Dias-Da-Silva, S., 2014. New postcranial elements of the Thalassodrominae (Pterodactyloidea, Tapejaridae) from the Romualdo Formation (Aptian–Albian), Santana Group, Araripe Basin, Brazil. Palaeontology 57 (2), 343–355.

Alarcón-Muñoz, J., Soto-Acuña, S., Codorniú, L., Rubilar-Rogers, D., Sallaberry, M., Suárez, M., 2020. New ctenochasmatid pterosaur record for Gondwana: discovery in the Lower Cretaceous continental deposits of the Atacama Desert, northern Chile. Cretac. Res. 110, 104378.

Alarcón-Muñoz, J., Codorniú, L., González, E., Suárez, M.E., Suárez, M., Vicencio-Campos, O., Soto-Acuña, S., Kaluza, J., Vargas, A.O., Rubilar-Rogers, D., 2022. A new locality with ctenochasmatid pterosaurs (Pterosauria: Pterodactyloidea) in the Atacama desert, northern Chile. Cretac. Res. 135, 105173.

Albuquerque, C., 2019, A Late Cretaceous Lonchodectid?: bioRxiv, p. 2019.2012.2017.879783.

Ambroggi, R., and De Lapparent, A., 1954, Les empreintes de pas fossiles du Maestrichtien d'Agadir: Notes et moires du Service de Mines et de la carte Geologique du Maroc, v. 10, p. 43-57.

Aires, A.S., Reichert, L.M., Müller, R.T., Pinheiro, F.L., Andrade, M.B., 2021. Development and evolution of the notarium in Pterosauria. J. Anat. 238 (2), 400–415.

Alarcón-Muñoz, J., Otero, R.A., Soto-Acuña, S., Vargas, A.O., Rojas, J., Rojas, O., 2021. First record of a Late Jurassic rhamphorhynchine pterosaur from Gondwana. Acta Palaeontol. Pol. 66 (3), 571–583.

Amiot, R., Wang, X., Lécuyer, C., Buffetaut, E., Boudad, L., Cavin, L., Ding, Z., Fluteau, F., Kellner, A.W., Tong, H., 2010. Oxygen and carbon isotope compositions of middle Cretaceous vertebrates from North Africa and Brazil: ecological and environmental significance: Palaeogeogr. Palaeoclimatol. Palaeoecol. 297 (2), 439–451.

Andres, B., 2021. Phylogenetic systematics of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea). J. Vertebr. Paleontol. 41 (sup1), 203–217.

Andres, B., Langston Jr., W., 2021. Morphology and taxonomy of *Quetzalcoatlus* Lawson 1975 (Pterodactyloidea: Azhdarchoidea). J. Vertebr. Paleontol. 41 (sup1), 46–202.

Andres, B., Qiang, J., 2006. A new species of *Istiodactylus* (pterosauria, pterodactyloidea) from the Lower Cretaceous of Liaoning, China. J. Vertebr. Paleontol. 26 (1), 70–78.

Andres, B., Qiang, J., 2008. A new pterosaur from the Liaoning Province of China, the phylogeny of the Pterodactyloidea, and convergence in their cervical vertebrae. Palaeontology 51 (2), 453–469.

Andres, B., Clark, J., Xu, X., 2014. The earliest pterodactyloid and the origin of the group. Curr. Biol. 24 (9), 1011–1016.

Andres, B., 2012, The early evolutionary history and adaptive radiation of the Pterosauria: Acta Geologica Sinica (English Edition), v. 86, no. 6, p. 1356-1365.

Apesteguía, S., 2007. The sauropod diversity of the La Amarga Formation (Barremian), Neuquén (Argentina). Gondwana Res. 12 (4), 533–546.

Apesteguía, S., Ösi, A., and Haluza, A., New pterosaur remains (Archosauria, Ornithodira) from the Late Cretaceous of Argentina and an evaluation of the Late Cretaceous South American record, *in* Proceedings Flugsaurier: pterosaur papers in honour of Peter Wellnhofer, München, Germany, 2007, Volume 23, p. 3R.

Arambourg, C., 1954, Sur la présence d'un ptérosaurien gigantesue dans les phosphates de Jordanie: Comptes rendus de l'Académie des Sciences, v. 238, no. 1, p. 133-134.

Assine, M., Perinotto, A., Custódio, M., Neumann, V.V., Mescolotti, P., 2014. Sequências deposicionais do Andar Alagoas da Bacia do Araripe, nordeste do Brasil. Boletim de Geociências da PETROBRAS 22 (1), 3–28.

Aureliano, T., Ghilardi, A.M., Duque, R.R., Barreto, A.M., 2014. On the occurrence of Pterosauria in Exu, Pernambuco (Lower Cretaceous Romualdo Formation, Araripe Basin), Northeastern Brazi. Estudos Geológicos 24 (2), 15–27.

Averianov, A., 2014. Review of taxonomy, geographic distribution, and paleoenvironments of Azhdarchidae (Pterosauria). ZooKeys 432, 1–107.

Averianov, A., 2020. Taxonomy of the Lonchodectidae (Pterosauria. Pterodactyloidea): Труды Зоологического института РАН 324 (1), 41–55.

Averianov, A., Arkhangelsky, M., Pervushov, E., Ivanov, A., 2005. A new record of an azhdarchid (Pterosauria: Azhdarchidae) from the Upper Cretaceous of the Volga Region: Paleontological Journal C/C of. Paleontol. Zh. 39 (4), 433.

Averianov, A.O., Arkhangelsky, M.S., 2020. A large pteranodontid pterosaur from the Late Cretaceous of Eastern Europe: Geol. Mag. 158 (7), 1143–1155.

Averianov, A.O., Kurin, A.S., 2022. A new specimen of pteranodontid pterosaur Bogolubovia orientalis from the upper cretaceous of Penza Province. Hist. Biol, Russia, pp. 1–9.

Bakhurina, N.N., Unwin, D.M., 1995. A survey of pterosaurs from the Jurassic and Cretaceous of the former. Soviet Union and Mongolia.

Bantim, R. A., Saraiva, A. A., Oliveira, G. R., and Sayão, J. M., 2014, A new toothed pterosaur (Pterodactyloidea: Anhangueridae) from the Early Cretaceous Romualdo Formation, NE Brazil: Zootaxa, v. 3869(3), 201–223.

Baron, M.G., 2021. The origin of Pterosaurs. Earth Sci. Rev. 221, 103777.

Barrett, P.M., Butler, R.J., Edwards, N.P., Milner, 2008. Pterosaur distribution in time and space: an atlas: Flugsaurier: pterosaur papers in honour of Peter Wellnhofer. Zitteliana B 28, 61–107.

Beccari, V., Pinheiro, F.L., Nunes, I., Anelli, L.E., Mateus, O., Costa, F.R., 2021. Osteology of an exceptionally well-preserved tapejarid skeleton from Brazil: Revealing the anatomy of a curious pterodactyloid clade. PLoS One 16 (8), e0254789.

Bell, C., Padian, K., 1995. Pterosaur fossils from the Cretaceous of Chile: evidence for a pterosaur colony on an inland desert plain: Geol. Mag. 132 (1), 31–38.

Bellardini, F., Codorniú, L., 2019. First Pterosaur Post-Cranial Remains from the Lower Cretaceous Lohan Cura Formation (Albian) of Patagonia, Argentina. Ameghiniana 56(2), 116–134.

Bellardini, F., 2016. Nuevos materiales de Pterodactyloidea (Pterosauria) de la Formación Lohan Cura (Albiano inferior) del suroeste de la Cuenca Neuquina, Patagonia, Argentina: Ameghiniana. Suplemento Resúmenes 53, 7.

Belvedere, M., Jalil, N.-E., Breda, A., Gattolin, G., Bourget, H., Khaldoune, F., Dyke, G.J., 2013. Vertebrate footprints from the Kem Kem beds (Morocco): A novel ichnological approach to faunal reconstruction: Palaeogeogr. Palaeoclimatol. Palaeoecol. 383, 52–58.

Bennett, S.C., 1989. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. J. Paleontol. 63 (5), 669–677.

Bennett, S.C., 1992. Sexual dimorphism of Pteranodon and other pterosaurs, with comments on cranial crests. J. Vertebr. Paleontol. 12 (4), 422–434.

Bennett, S.C., 1995. A statistical study of *Rhamphorhynchus* from the Solnhofen Limestone of Germany: year-classes of a single large species. J. Paleontol. 69 (3), 569–580.

Bennett, S.C., 2001. The osteology and functional morphology of the Late Cretaceous pterosaur *Pteranodon* Part I. General description of osteology. Palaeontographica Abteilung A, pp. 1–112.

Bennett, S.C., Long, J.A., 1991. A large pterodactyloid pterosaur from the Late Cretaceous (Late Maastrichtian) of Western Australia. Records of the Western Australian Museum 15 (2), 435–443.

Benton, M.J., Bouaziz, S., Buffetaut, E., Martill, D., Ouaja, M., Soussi, M., Trueman, C., 2000. Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 157 (3–4), 227–246.

Benyoucef, M., Pérez-García, A., Bendella, M., Ortega, F., Vullo, R., Bouchemla, I., Ferré, B., 2022. The "mid"-Cretaceous (Lower Cenomanian) Continental Vertebrates of Gara Samani, Algeria. Sedimentological Framework and Palaeodiversity: Frontiers in Earth Sci. 10.

Bertozzo, F., Da Silva, B.C., Martill, D., Marlene, E., Vorderwuelbecke, T.A., Schouten, R., and Aquino, P., 2021, A large pterosaur femur from the Kimmeridgian, Upper Jurassic of Lusitanian Basin, Portugal, Acta Palaeontol. Pol. 66(4), 815–825.

Bestwick, J., Unwin, D.M., Butler, R. J. H., Donald H., and Purnell, M., 2018b, Dental microwear textural analysis: reconstructing diets of non-mammalian fossil taxa from the Solnhofen archipelago: PalAss 62nd Ann., p. 68–69.

Bestwick, J., Unwin, D.M., Butler, R.J., Henderson, D.M., Purnell, M.A., 2018a. Pterosaur dietary hypotheses: a review of ideas and approaches: Biol. Rev. 93 (4), 2021–2048.

Beurlen, K., 1963, Geologia e estratigrafia da Chapada do Araripe. In: Congresso Brasileiro de Geologia, 17., 1963, Recife. Anais. Recife: Sociedade Brasileira de Geologia/Sudene, 1963. Suplementos, p. 47.

Blackbeard, M., Yates, A., 2007. The taphonomy of an Early Jurassic dinosaur bonebed in the Northern Free State (South Africa), *in*. Proceedings Journal of Vertebrate Paleontology 27, 49A.

Blackburn, D., 2002, Two Early Cretaceous pterosaurs from Africa: J. Vertebr. Paleontol., v. 22.

Bogolyubov, N., 1914, On the pterodactyl vertebra from the Upper Cretaceous deposits of Saratov Province: Ezhegodnik po Geologii i Mineralogii Rossii, v. 16, p. 1-7.
Bonaparte, J., 1970. Bonaparte 1970 *Pterodaustro guinazui* gen. et sp. nov. Pterosaurio de la Formacion Lagarcito, Provincia de San Luis, Argentina. Acta Geológica Lilloana 10 (10), 207–226.
Bonaparte, J.F., 1978. El Mesozoico de América del Sur y sus tetrápodos. Ministerio de Cultura y Educación, Fundación Miguel Lillo.
Bonaparte, J., Sánchez, T., 1975. Restos de un pterosaurio, *Puntanipterus globosus*, de la Formación La Cruz, provincia de San Luis, Argentina, *in*. Proceedings Actas Primo Congresso Argentino de Paleontologia e Biostratigraphia 2, 105–113.
Bonaparte, J., Schultz, C., and Soares, M., 2010, Pterosauria from the Late Triassic of southern Brazil. New aspects of Mesozoic biodiversity, p. 63–71.
Bonaparte, J., 1971. Descripción del cráneo y mandíbulas de *Pterodaustro guiñazui*, (Pterodactyloidea, Pterodaustriidae nov.) de la Formación Lagarcito, San Luis, Argentina. Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata 1 (9), 263–272.
Bordy, E.M., Abrahams, M., Sharman, G.R., Viglietti, P.A., Benson, R.B., McPhee, B.W., Barrett, P.M., Sciscio, L., Condon, D., Mundil, R., 2020. A chronostratigraphic framework for the upper Stormberg Group: implications for the Triassic-Jurassic boundary in southern Africa. Earth Sci. Rev. 203, 103120.
Brito, P.M., Yabumoto, Y., 2011. An updated review of the fish faunas from the Crato and Santana formations in Brazil, a close relationship to the Tethys fauna. Bull. Kitakyushu Mus. Nat. Hist. Hum. Hist. A. 9, 107–136.
Britto, D. d. M. M., Piovesan, E. K., da Silveira, D. M., Fallgatter, C., and Grillo, J., 2022, Early Cretaceous non-marine ostracods from the Recôncavo Basin, Northeast of Brazil: J. S. Am. Earth Sci., v. 116, p. 103841.
Brougham, T., Smith, E. T., and Bell, P. R., 2017, Isolated teeth of Anhangueria (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Lightning Ridge, New South Wales, Australia: PeerJ 5, e3256.
Buchmann, R., Avilla, L. d. S., and Rodrigues, T., 2019, Comparative analysis of the vertebral pneumatization in pterosaurs (Reptilia: Pterosauria) and extant birds (Avialae: Neornithes): PLOS ONE, v. 14, no. 10, p. e0224165.
Buchmann, R., Rodrigues, T., Polegario, S., Kellner, A.W.A., 2017. New information on the postcranial skeleton of the Thalassodrominae (Pterosauria, Pterodactyloidea, Tapejaridae). Hist. Biol. 30 (8), 1139–1149.
Buchmann, R., Holgado, B., Sobral, G., dos Santos Avilla, L., Rodrigues, T., 2021. Quantitative assessment of the vertebral pneumaticity in an anhanguerid pterosaur using micro-CT scanning:. Sci. Rep. 11 (1), 18718.
Burch, S., and Sertich, J., 2011, Giant pterosaur remains from the Campanian of the Morondava Basin, western Madagascar: J. Vertebr. Paleontol., v. 31, no. 3: supp., p. 80A. Presented at 71st SVP Meeting in Las Vegas.
Cadena, E.A., Unwin, D.M., Martill, D.M., 2020. Lower Cretaceous pterosaurs from Colombia: Cretac. Res. 114, 104526.
Cahen, L., 1954, Géologie du Congo belge, Impr. H. Vaillant-Carmanne.
Cai, Z., Wei, F., 1993. On a new pterosaur (Zhejiangopterus linhaiensis gen. et sp. In: nov.) from Upper Cretaceous in Linhai, Zhjiang, China. Vertebrata Palasiatica 32, 181–194.
Calvo, J.O., Lockley, M.G., 2001. The first pterosaur tracks from Gondwana: Cretac. Res. 22 (5), 585–590.
Campos, D. d. A., and Kellner, A., 1985a, Panorama of the flying reptiles study in Brazil and South America: Anais da Academia Brasileira de Ciências, v. 57, no. 4, p. 453-466.
Campos, D. d. A., and Kellner, A., 1985b, Um novo exemplar de *Anhanguera blittersdorffi* (Reptilia, Pterosauria) da formação Santana, Cretáceo Inferior do Nordeste do Brasil: Resumo das Comun. do IX Congo Brasil. Paleont, v. 13.
Campos, D.d.A., Kellner, A., 1997. Short note on the first occurrence of Tapejaridae in the Crato Member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil. Anais Academia Brasileira de Ciencias 69, 83–88.
Campos, H.B.N., Kischlat, E.E., 2020. The tapejarid pterosaur *Tupandactylus imperator* from Crato Formation and the preservation of cranial integuments. BioRxiv, 1–21.
Campos, H. B. N., Cincotta, A., Frey, E., Godefroit, P., and Yans, J., 2017, A unique exceptionally well-preserved pterosaur skull from the Crato Formation of Brazil: PeerJ Preprints.
Campos, D. d. A., Ligabue, D., and Taquet, P., 1984. Wing membrane and wing supporting fibers of a flying reptile from the Lower Cretaceous of the Chapada do Araripe (Aptian; Ceará State, Brazil), *in* Proceedings Proc. 3rd Symp. Mesozoic Terrestrial Ecosystems, Short Papers (eds Reif E., Westphal F.) 3 p. 37-39.
Casamiquela, R.M., 1975. *Herbstosaurus pigmaeus* (Coeluria, Compsognathidae) n. gen. n. sp. del Jurásic medio del Neuquén (Patagonia septentrional). Uno de los más pequeños dinosaurios conocidos [Herbstosaurus pigmaeus (Coeluria, Compsognathidae) n. gen. n. sp. from the Middle Jurassic of Neuquén (northern Patagonia). One of the smallest known dinosaurs]: Actas del Primer Congreso Argentino de Paleontologia y Bioestratigrafia, Tucumán 2, 87–102.
Casamiquela, R.M., Diaz, 1980. La presencia de *Pterodaustro* Bonaparte (Pterodactyloidea), del Neojurásico (?) de la Argentina, en los Andes del Norte de Chile, *in*. Proceedings Congreso Argentino de Paleontología y Bioestratigrafía. No. 2, 201–213.
Cerqueira, G.M., Müller, R.T., Pinheiro, 2023. On the phylogenetic affinities of the tapejarid pterosaur 'Tupuxuara deliradamus' from the Lower Cretaceous of Brazil: Hist. Biol, 1–6.
Cerqueira, G.M., Santos, M.A., Marks, M.F., Sayão, J.M., Pinheiro, F.L., 2021. A new azhdarchoid pterosaur from the Lower Cretaceous of Brazil and the paleobiogeography of the Tapejaridae:. Acta Palaeontol. Pol. 66 (3), 555–570.
Cheng, X., Jiang, S., Wang, X., Kellner, A.W., 2016. New information on the Wukongopteridae (Pterosauria) revealed by a new specimen from the Jurassic of China. PeerJ 4, e2177.
Chiappe, L., Chinsamy, A., 1996. *Pterodaustro's* true teeth. Nature 379 (6562), 211.
Chiappe, L.M., Codorniú, L., Grellet-Tinner, G., Rivarola, D., 2004. Argentinian unhatched pterosaur fossil. Nature 432 (7017), 571–572.
Chiappe, L., Rivariola, D., Cione, A., Fregenal-Martínez, M., Sozzi, H., Buatois, L., Gallego, O., Laza, J., Romero, E., López-Arbarello, A. B., A, Marsicano, C., Adamonis, S., Ortega, F., McGehee, S., and Di Iorio, O., 1998a, Biotic association and paleoenvironmental reconstruction of the "Loma del *Pterodaustro*" fossil site (Early Cretaceous, Argentina): Geobios, v. 31, no. 3, p. 349–369.
Chiappe, L., Rivarola, D., Romero, E., Davila, S., Codorniu, L., 1998b. Recent advances in the paleontology of the Lower Cretaceous Lagarcito Formation (Parque Nacional Sierra de Las Quijadas, San Luis; Argentina): New Mex. Mus. Nat. Hist. Sci Bull. 14, 187–192.
Chiappe, L., Kellner, A., Rivarola, D., 2000. Cranial morphology of *Pterodaustro guinazui* (Pterosauria: Pterodactyloidea) from the Lower Cretaceous of Argentina. Contrib. in Sci. 483, 1–19.
Chinsamy, A., Codorniú, L., Chiappe, L., 2008. Developmental growth patterns of the filter-feeder pterosaur *Pterodaustro guinazui*. : Biol. Lett. 4 (3), 282–285.
Chinsamy, A., Codorniú, L., Chiappe, L., 2009. Palaeobiological implications of the bone histology of *Pterodaustro guinazui*:. Anat. Rec. 292 (9), 1462–1477.
Codorniú, L., and Gasparini, Z., 2007, Pterosauria, *in* Gasparini, Z., Salgado, L., and Coria, R. A., eds., Patagonian Mesozoic Reptiles: Bloomington and Indianapolis, Indiana Indiana University Press, p. 143-166.
Codorniú, L., and Gianechini, F. A., 2016, The flying reptiles from Argentina: an overview: Jornadas Argentinas de Paleontología de Vertebrados, v. 6, no. 1, p. 1666-5503.
Codorniú, L., Chiappe, L.M., 2004a. Early juvenile pterosaurs (Pterodactyloidea: *Pterodaustro guinazui*) from the Lower Cretaceous of central Argentina: Can. J. Earth Sci. 41 (1), 9–18.
Codorniú, L., Chiappe, L.M., 2004b. Early juvenile pterosaurs (Pterodactyloidea: *Pterodaustro guinazui*) from the Lower Cretaceous of central Argentina. Can. J. Earth Sci. 41 (1), 9–18.
Codorniú, L.S., Gasparini, Z., 2012. The Late Jurassic pterosaurs from northern Patagonia, Argentina. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 103 (3–4), 399–408.
Codorniú, L., Gasparini, Z., Paulina-Carabajal, A., 2006. A Late Jurassic pterosaur (Reptilia, Pterodactyloidea) from northwestern Patagonia, Argentina. J. S. Am. Earth Sci. 20 (4), 383–389.
Codorniú, L., Rauhut, O., Pol, D., 2010. Osteological features of Middle Jurassic Pterosaurs from Patagonia (Argentina). Acta Geosci. Sin. 31 (1), 12–13.
Codorniú, L., Pol, D., Rauhut, O., Paulina-Carabajal, A., 2011. The braincase of a 3D preserved pterosaur from the Jurassic of Patagonia. Ameghiniana 48 (4), 155R.
Codorniú, L., Chiappe, L.M., Cid, F.D., 2013. First occurrence of stomach stones in pterosaurs. J. Vertebr. Paleontol. 33 (3), 647–654.
Codorniú, L., Carabajal, A.P., Pol, D., Unwin, D., Rauhut, O.W., 2016a. A Jurassic pterosaur from Patagonia and the origin of the pterodactyloid neurocranium. PeerJ 4, e2311.
Codorniú, L., Paulina-Carabajal, A., Gianechini, F.A., 2016b. Braincase anatomy of *Pterodaustro guinazui*, pterodactyloid pterosaur from the Lower Cretaceous of Argentina. J. Vertebr. Paleontol. 36 (1), e1031340.
Codorniú, L., Chiappe, L., Rivarola, D., 2017. Neonate morphology and development in pterosaurs: evidence from a Ctenochasmatid embryo from the Early Cretaceous of Argentina: Geol. Soc. Lond. Spec. 455 (1) 83–94.
Codorniú, L., Garrido, A., 2013. New fossil record of a Jurassic pterosaur from Neuquen Basin, Vaca Muerta Formation, Argentina. J. S. Am. Earth Sci. 48, 315–321.
Colbert, E.H., 1969. Jurassic pterosaur from Cuba: Am. Mus. Novit. 2370, 1–26.
Collini, C. A., 1784, Sur quelques Zoolithes du Cabinet d'Histoire naturelle de S.A.S.E. Palatine & de Bavière, à Mannheim: Acta Academiae Theodoro Palatinae, Mannheim, Pars Physica, v. 5, p. 58-103.
Cope, E.D., 1871. On two new ornithosaurians from Kansas: Proc. Am. Phil. Soc. 12 (86), 420–422.
Costa, F.R., Kellner, A.W., 2009. On two pterosaur humeri from the Tendaguru beds (Upper Jurassic, Tanzania). An. Acad. Bras. Cienc. 81 (4), 813–818.
Costa, F.R., Sayão, J.M., Kellner, A.W.A., 2015. New pterosaur material from the Upper Jurassic of Tendaguru (Tanzania), Africa: Hist. Biol. 27 (6), 646–655.
Cruzado-Caballero, P., Méndez, A., Filippi, L., Juárez Valieri, R., Garrido, A., 2016. Palaeobiodiversity of the Bajo de la Carpa Formation (Santonian, Upper Cretaceous) in the Cerro Overo-La Invernada area, northern Patagonia, Argentina: VII Jornadas internacionales sobre paleontología de dinosaurios y su entorno. Salas. de los Infantes. Burgos, España, p. 53.
Cuvier, G., 1809. Mémoire sur le squelette fossile d'un reptile volant des environs d'Aichstedt, que quelques naturalistes ont pris pour un oiseau, et dont nous formons un genre de Sauriens, sous le nom de Ptero-Dactyle, *in*. Proceedings Annales du Muséum national d'Histoire Naturelle, Paris 13, 424–437.
Dal Sasso, C., Pasini, G., 2003. First record of pterosaurs (Diapsida, Archosauromorpha, Pterosauria) in the Middle Jurassic of Madagascar: Atti della Società italiana di scienze naturali e del museo civico di storia naturale di. Milano 144 (2), 281–296.

Dalla Vecchia, F., 1993. *Cearadactylus*? *ligabuei* nov. sp., a new early Cretaceous (Aptian) pterosaur from Chapada do Araripe (Northeastern Brazil). Bollettino della Società paleontologica italiana 32 (3), 401–409.
Dalla Vecchia, F.M., 2019. *Seazzadactylus venieri* gen. et sp. nov., a new pterosaur (Diapsida: Pterosauria) from the Upper Triassic (Norian) of northeastern Italy. PeerJ 7, e7363.
Dalla Vecchia, F.M., Arduini, P., Kellner, A.W., 2001. The first pterosaur from the Cenomanian (Late Cretaceous) Lagerstätten of Lebanon: Cretac. Res. 22 (2), 219–225.
Dalla Vecchia, Riera, V., Oms, J.O., Dinarès-Turell, J., Gaete, R., Galobart, A., 2013. The last pterosaurs: first record from the uppermost Maastrichtian of the Tremp Syncline (northern Spain). Acta Geologica Sinica (English Edition) 87 (5), 1198–1227.
Dalla Vecchia, F. M., 2013, Triassic pterosaurs, *in* Nesbitt, S. J., and Desojo, J. B. I., R.B., eds., Anatomy, phylogeny, and palaeobiology of early archosaurs and their kin, Volume 379: London, UK, Geological Society of London, Special Publications, p. 119–155.
Dávila, S., Chiappe, L., Rivarola, D., 1999. Anatomía pélvica y miembros posteriores de pterosaurios del Cretácico de la Provincia de San Luis. Ameghiniana 36, R98.
De Buisonjé, P., 1981. *Santanadactylus brasilensis : Gea* 14 (2), 37–48.
De Buisonjé, P., 1980. *Santanadactylus brasilensis* nov gen, nov sp, A Long Necked, Large Pterosaur From The Aptian Of Brasil. 1. Proceedings of the Koninklijke Nederlandse Akademie Van Wetenschappen Series B Palaeontology Geology Physics Chemistry Anthropology 83 (2), 145–157.
De Ricqlès, A.J., Padian, K., Horner, J.R., Francillon-Vieillot, H., 2000. Palaeohistology of the bones of pterosaurs (Reptilia: Archosauria): anatomy, ontogeny, and biomechanical implications: Zool. J. Linn. Soc. 129 (3), 349–385.
Díaz-Martínez, I., Heredia, A.M., González, S.N., Canale, N., de Valais, S., Cónsole-Gonella, C.A., Montes, R.M., Caratelli, M., Urzagasti-Torres, S., Fischer, G., Lecuona, A., Paniceres, P., Salgado, L., Citton, P., 2022. Pterosaur Tracks from the Upper Cretaceous Anacleto Formation (Neuquén Basin), Northern Patagonia, Argentina: Insights into Campanian Pterosaur Diversity in Gondwana. : Diversity 14 (11), 1007.
Dong, Z., Sun, Y., Wu, S., 2003. On a new pterosaur from the Lower Cretaceous of Chaoyang Basin, western Liaoning, China: Glob. Geol. 22 (1), 1–7.
Dubey, V., Narain, K., 1946. A note on the occurrence of Pterosauria in India: Curr. Sci. 15 (10), 287–288.
Duque, R.R.C., Pinheiro, F.L., Barreto, 2022. The ontogenetic growth of Anhangueridae (Pterosauria, Pterodactyloidea) premaxillary crests as revealed by a crestless *Anhanguera* specimen. J. Vertebr. Paleontol. 42, (1) e2116984.
Eaton, G.F., 1910. Osteology of *Pteranodon*: Mem. Conn. Acad. Arts Sci. 2, 1–38.
Eck, K., Elgin, R.A., Frey, E., 2011. On the osteology of *Tapejara wellnhoferi* Kellner 1989 and the first occurrence of a multiple specimen assemblage from the Santana Formation, Araripe Basin, NE Brazil:. Swiss Journal of Palaeontology 130 (2), 277–296.
Edmund, A.G., 1960. Tooth replacement phenomena in the lower vertebrates. R. Ontario Mus. Contrib. Life Sci. Div. 52, 1–90.
Elgin, R. A., and Frey, E., 2011a, A new ornithocheirid, *Barbosania gracilirostris* gen. et sp. nov.(Pterosauria, Pterodactyloidea) from the Santana Formation (Cretaceous) of NE Brazil: Swiss J. Palaeontol., v. 130, no. 2, p. 259.
Elgin, R., Campos, H., 2012. A new specimen of the azhdarchoid pterosaur *Tapejara wellnhoferi*: Hist. Biol. 24 (6), 586–591.
Elgin, R.A., Frey, E., 2011. A new azhdarchoid pterosaur from the Cenomanian (Late Cretaceous) of Lebanon: Swiss. J. Geosci. 104 (1), 21–33.
Elgin, R.A., Frey, E., 2012. A nearly complete ornithocheirid pterosaur from the Crato Formation (Aptian. Early Cretaceous) of NE Brazil.
Elgin, R.A., Hone, D.W.E., 2013. Pneumatization of an immature azhdarchoid pterosaur: Cretac. Res. 45, 16–24.
Elias, F.A., Bertini, R.J., Medeiros, M.A.A., 2007. Pterosaur teeth from the Laje do Coringa, middle Cretaceous. São Luís Grajaú basin, Maranhão state, Northern-Northeastern Brazil: Brazilian Journal of Geology 37 (4), 668–676.
Ezcurra, M., Nesbitt, S., Bronzati, M., Dalla Vecchia, F., Agnolin, F., Benson, R., Egli, F., Cabreira, S., Evers, S., Gentil, A., 2020. Enigmatic dinosaur precursors bridge the gap to the origin of Pterosauria. Nature 588 (7838), 445–449.
Fanti, F., Miyashita, T., Cantelli, L., Mnasri, F., Dridi, J., Contessi, M., Cau, A., 2016. The largest thalattosuchian (Crocodylomorpha) supports teleosaurid survival across the Jurassic-Cretaceous boundary: Cretac. Res. 61, 263–274.
Fastnacht, M., 2001. First record of *Coloborhynchus* (Pterosauria) from the Santana Formation (Lower Cretaceous) of the Chapada do Araripe, Brazil. Paläontol. Z. 75 (1), 23–36.
Fernandes, A.E., Mateus, O., Andres, B., Polcyn, M.J., Schulp, A.S., Gonçalves, A.O., Jacobs, L.L., 2022. Pterosaurs from the Late Cretaceous of Angola. Diversity 14 (9), 741.
Fletcher, T.L., Salisbury, S.W., 2010. New pterosaur fossils from the Early Cretaceous (Albian) of Queensland, Australia. J. Vertebr. Paleontol. 30 (6), 1747–1759.
Frey, E., Martill, D., 1994. A new pterosaur from the Crato Formation (Lower Cretaceous, Aptian) of Brazil. : Neues Jahrbuch fur Geologie und Palaontologie Abhandlungen 194 (2), 379–412.
Frey, E., Martill, D., 1996. A reappraisal of *Arambourgiania* (Pterosauria, Pterodactyloidea): one of the world's largest flying animals. Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen 199 (2), 221–247.
Frey, E., Martill, D.M., Buchy, M.C., 2003a. A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur: Geol. Soc. Lond. Spec. 217 (1), 55–63.
Frey, E., Martill, D.M., Buchy, M.C., 2003b. A new species of tapejarid pterosaur with soft-tissue head crest: Geol. Soc. Lond. Spec. 217 (1), 65–72.
Frey, E., Tischlinger, H., Buchy, M.C., Martill, D.M., 2003c. New specimens of Pterosauria (Reptilia) with soft parts with implications for pterosaurian anatomy and locomotion: Geol. Soc. Lond. Spec. 217 (1), 233–266.
Galton, P.M., 1980. Avian-like tibiotarsi of pterodactyloids (Reptilia: Pterosauria) from the Upper Jurassic of East Africa. Paläontol. Z. 54 (3–4), 331–342.
Gasparini, Z., Leanza, H.A., Zubillaga, J.I.G., 1987. Un pterosaurio de las calizas litográficas tithonianas del área de Los Catutos, Neuquén, Argentina. Ameghiniana, 24 (1-2), 141-143.
Grellet-Tinner, G., Thompson, M.B., Fiorelli, L.E., Argañaraz, E., Codorniú, L., Hechenleitner, E.M., 2014. The first pterosaur 3-D egg: Implications for *Pterodaustro guinazui* nesting strategies, an Albian filter feeder pterosaur from central Argentina:. Geosci. Front. 5 (6), 759–765.
Haddoumi, H., Allain, R., Meslouh, S., Metais, G., Monbaron, M., Pons, D., Rage, J.C., Vullo, R., Zouhri, S., Gheerbrant, E., 2016. Guelb el Ahmar (Bathonian, Anoual Syncline, eastern Morocco): first continental flora and fauna including mammals from the Middle Jurassic of Africa. Gondwana Res. 29 (1), 290–319.
Haluza, A., Apesteguía, S., Makovicky, P.J., 2007. Pterosaur remains (Archosauria, Ornithodira) from the early Late Cretaceous of "La Buitrera", Río Negro, Argentina. : Ameghiniana 44 (4), 22R.
Haluza, A., Canale, J., 2009. A new pterosaur remain from the Neuquén Group. Late Cretaceous of Patagonia: Ameghiniana 46 (4), 31R.
Hammer, W.R., Hickerson, W.J., 1994. A crested theropod dinosaur from Antarctica:. Science 264 (5160), 828–830.
Hammer, W., Hickerson, W., 1996. Implications of an Early Jurassic vertebrate fauna from Antarctica: The Continental Jurassic. Mus. North. Ariz. Bull. 60, 215–218.
Hammer, W.R., Hickerson, W.J., 1999. Gondwana dinosaurs from the Jurassic of Antarctica:. Natl. Sci. Mus. Monogr. 15, 211–217.
Headden, J.A., Campos, H.B., 2015. An unusual edentulous pterosaur from the Early Cretaceous Romualdo Formation of Brazil:. Hist. Biol. 27 (7), 815–826.
Heimhofer, U., Ariztegui, D., Lenniger, M., Hesselbo, S. P., Martill, D. M., and Rios Netto, A. M., 2010, Deciphering the depositional environment of the laminated Crato fossil beds (Early Cretaceous, Araripe Basin, North-eastern Brazil): Sedimentology, v. 57, no. 2, p. 677-694.
Herne, M.C., Nair, J.P., Salisbury, S.W., 2010. Comment on "A southern tyrant reptile". Science 329 (5995), 1013.
Hocknull, S. A., and Cook, A. G., 2007, Flights of fancy! On the trail of the elusive Aussie pterosaurs: Australian Age of Dinosaurs Museum of Natural History Annual, v. 5, p. 26–35.
Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A.G., Calleja, N.D., Sloan, T., Elliott, D. A., 2009. New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. PLoS One 4 (7), e6190.
Holgado, B., Pêgas, R.V., 2020. A taxonomic and phylogenetic review of the anhanguerid pterosaur group Coloborhynchinae and the new clade Tropeognathinae:. Acta Palaeontol. Pol. 65 (4), 743–761.
Hone, D.W.E., 2020. A Review of the Taxonomy and Palaeoecology of the Anurognathidae (Reptilia, Pterosauria). Acta Geologica Sinica English Edition 94 (5), 1676–1692.
Howse, S., Milner, A., and Martill, D., 2001, Pterosaurs: Dinosaurs of the Isle of Wight, v. 10, p. 324-335.
Humphries, S., Bonser, R.H., Witton, M.P., Martill, D.M., 2007. Did pterosaurs feed by skimming? Physical modelling and anatomical evaluation of an unusual feeding method. PLoS Biology 5 (8), e204.
Hwang, K.G., Huh, M., Lockley, M.G., Unwin, D.M., Wright, J.L., 2002. New pterosaur tracks (Pteraichnidae) from the Late Cretaceous Uhangri Formation, southwestern Korea:. Geol. Mag. 139 (4), 421–435.
Hyder, E.S., Witton, M.P., Martill, D.M., 2014. Evolution of the pterosaur pelvis:. Acta Palaeontol. Pol. 59 (1), 109–124.
Ibiricu, L.M., Casal, G.A., Martínez, R.D., Alvarez, B.N., Poropat, 2019. New materials and an overview of Cretaceous vertebrates from the Chubut Group of the Golfo San Jorge Basin, central Patagonia, Argentina. J. S. Am. Earth Sci. 98, 102460.
Ibiricu, L.M., Martínez, R.D., Casal, G.A., 2012. The first record of Pterosauria in the Bajo Barreal Formation (Upper Cretaceous), central Patagonia, Argentina. Ameghiniana 49 (4), 657–661.
Ibrahim, N., Unwin, D.M., Martill, D.M., Baidder, L., Zouhri, S., 2010. A new pterosaur (Pterodactyloidea: Azhdarchidae) from the Upper Cretaceous of Morocco. PLoS One 5 (5), e10875.
Ibrahim, N., Sereno, P.C., Varricchio, D.J., Martill, D.M., Dutheil, D.B., Unwin, D.M., Baidder, L., Larsson, H.C., Zouhri, S., Kaoukaya, A., 2020. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. ZooKeys 928, 1.
Jacobs, M.L., Martill, D.M., Ibrahim, N., Longrich, N., 2019. A new species of *Coloborhynchus* (Pterosauria, Ornithocheiridae) from the mid-Cretaceous of North Africa:. Cretac. Res. 95, 77–88.
Jacobs, M.L., Martill, D.M., Unwin, D.M., Ibrahim, N., Zouhri, S., Longrich, N.R., 2020. New toothed pterosaurs (Pterosauria: Ornithocheiridae) from the middle Cretaceous Kem Kem beds of Morocco and implications for pterosaur palaeobiogeography and diversity:. Cretac. Res. 110, 104413.
Jain, S. L., 1974, Jurassic pterosaur from India: Geological Society of India, v. 15, no. 3, p. 330-335.
Janensch, W., 1914, Die Gliederung der Tendaguru Schichten im Tendaguru Gebiet und die Entstehung der SaurierLagerstätten: Archiv für Biontologie, v. 3, no. 3, p. 227-261.
Ji, S.A., 2020. First record of Early Cretaceous pterosaur from the Ordos Region, Inner Mongolia, China:. Chin. Geol. 3 (1), 1–7.

Kaddumi, H., 2006. A new genus and species of gigantic marine turtles (Chelonioidea: Cheloniidae) from the Maastrichtian of the Harrana Fauna-Jordan. PalArch 3, 1–13.
Kaddumi, H., 2009. On the remains of the first pterosaur (Ornithocheiroidea: Nyctosauridae) from the Muwaqqar Chalk Marl Formation of Harrana. In: Kaddumi, H. (Ed.), Fossils of the Harrana Fauna and the Adjacent Areas. Publications of the Eternal River Museum of Natural History, Amman, pp. 241–247.
Kear, B.P., Deacon, G.L., Siverson, M., 2010. Remains of a Late Cretaceous pterosaur from the Molecap Greensand of Western Australia. Alcheringa 34 (3), 273–279.
Kellner, A., 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, Northeast Brazil. Anais da Academia brasileira de Ciências 61 (4), 439–446.
Kellner, A., 1994. Remarks on pterosaur taphonomy and paleoecology. Acta Geologica Leopoldensia 39 (1), 175–189.
Kellner, A., 1995. The relationships of the Tapejaridae (Pterodactyloidea) with comments on pterosaur phylogeny, *in* Proceedings Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota Short Papers. China Ocean Press, Beijing, pp. 73–77.
Kellner, A., 1996. Description of new material of Tapejaridae and Anhangueridae (Pterosauria, Pterodactyloidea) and discussion of pterosaur phylogeny, Ph.D. Thesis. Columbia University, p. 347.
Kellner, A., 2001a. A new hypothesis of pterosaur phylogeny: I e II Simpósios sobre a Bacia do Araripe e bacias interiores do Nordeste. Comunicações. Crato, 249–258.
Kellner, A., 2001b. A review of the pterosaur record from Gondwana. Strata 11, 51–53.
Kellner, A.W., 2003a. Pterosaur phylogeny and comments on the evolutionary history of the group: Geol. Soc. Lond. Spec. 217 (1), 105–137.
Kellner, A.W., 2013. A new unusual tapejarid (Pterosauria, Pterodactyloidea) from the Early Cretaceous Romualdo Formation, Araripe Basin, Brazil:. Earth Environ. Sci. T Roy. Soc. Edinb. 103 (3–4), 409–421.
Kellner, A.W., 2015. Comments on Triassic pterosaurs with discussion about ontogeny and description of new taxa. An. Acad. Bras. Cienc. 87 (2), 669–689.
Kellner, A., 2019. A reconstrução do Museu Nacional: bom para o Rio, bom para o Brasil! Ciência e Cultura 71 (3), 4–5.
Kellner, A., 1984. Ocorrência de uma mandibula de Pterosauria (Brasileodactylus araripensis nov. gen.; nov. sp.) na formação Santana, in Proceedings Cretáceo da chapada do Araripe, Ceará Brasil XXXIII. Anais Congresso Brasileiro de Geologia, Rio de Janeiro1984, 578–590.
Kellner, A.W., Aguirre-Urreta, M.B., Ramos, V.A., 2003. On the pterosaur remains from the Río Belgrano formation (Barremian), Patagonian Andes of Argentina. An. Acad. Bras. Cienc. 75 (4), 487–495.
Kellner, A.W.A., Calvo, J., 2017. New azhdarchoid pterosaur (Pterosauria, Pterodactyloidea) with an unusual lower jaw from the Portezuelo Formation (Upper Cretaceous), Neuquén Group, Patagonia, Argentina. Annals of the Brazilian Academy of Sciences 89, 2003–2012.
Kellner, A., and Mader, B., 1996, First report of pterosauria (Pterodactyloidea, Azhdarchidae) from Cretaceous rocks of Morocco: Department of Vertebrate Paleontology and Department of Mammalogy, American Museum of Natural History, Central Park West at 79th St., New York, NY 10024-5192, v. 16, no. 3, p. 45A.
Kellner, A.W.A., Caldwell, M.W., Holgado, B., Vecchia, F.M.D., Nohra, R., Sayão, J.M., Currie, P.J., 2019a. First complete pterosaur from the Afro-Arabian continent: insight into pterodactyloid diversity: Sci. Rep. 9 (1), 1–9.
Kellner, A., Calvo, J., Sayão, J., Porfiri, J., 2004. First pterosaur from the Portezuelo Formation, Neuquén Group, Patagonia, Argentina: 4° Simpósio Brasileiro de Paleontología de Vertebrados. Resumos, 29–30.
Kellner, A.W., Calvo, J.O., Sayão, J.M., Porfiri, J.D., 2006. Pterosaur bones from the Portezuelo Formation (Cretaceous), Neuquén Group, Patagonia, Argentina. Arquivos do Museu Nacional 64 (4), 369–375.
Kellner, A.W.A., Campos, D.d.A., 2007b. Short note on the ingroup relationships of the Tapejaridae (Pterosauria, Pterodactyloidea). Boletim do Museu Nacional 75, 1–14.
Kellner, A., and Campos, D. d. A., 1988, Sobre um novo Pterossauro com crista sagital da Bacia do Araripe, Cretáceo Inferior do Nordeste do Brasil: Anais da Academia Brasileira de Ciências, v. 60, no. 4, p. 459-469.
Kellner, A. W., and Campos, D. d. A., 1994, A new species of Tupuxuara (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil: Anais da Academia Brasileira de Ciências, v. 66, no. 4, p. 467-474.
Kellner, A. W., and Campos, D. d. A., 2002, The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil: Science, v. 297, no. 5580, p. 389-392.
Kellner, A., Mello, A., Ford, T., Carvalho, I., Cassab, R., Schwanke, C., Carvalho, M., Fernandes, A., Rodrigues, M., and Carvalho, M., 2007. A survey of pterosaurs from Africa with the description of a new specimen from Morocco: Paleontologia: Cenarios de Vida, p. 257-267.
Kellner, A.W., Campos, D.A., Sayao, J.M., Saraiva, A.A., Rodrigues, T., Oliveira, G., Cruz, L.A., Costa, F.R., Silva, H.P., Ferreira, 2013. The largest flying reptile from Gondwana: a new specimen of *Tropeognathus* cf. *T. mesembrinus* Wellnhofer, 1987 (Pterodactyloidea, Anhangueridae) and other large pterosaurs from the Romualdo Formation, Lower Cretaceous, Brazil. Anais da Academia Brasileira de Ciências 85 (1), 113–135.
Kellner, A. W. A., Rodrigues, T., Costa, F. R., Weinschütz, L. C., Figueiredo, R. G., Souza, G. A. D., Brum, A. S., Eleutério, L. H. S., Mueller, C. W., and Sayão, J. M., 2019b, Pterodactyloid pterosaur bones from Cretaceous deposits of the Antarctic Peninsula: Anais da Academia Brasileira de Ciências, v. 91.
Kellner, A., Hasegawa, Y., 1993. Postcranial skeleton of *Tupuxuara* (Pterosauria, Pterodactyloidea, Tapejaridae) from the Lower Cretaceous of Brazil. J. Vertebr. Paleontol. 13 (3), 44A.
Kellner, A.W., Mader, B.J., 1997. Archosaur teeth from the Cretaceous of Morocco. J. Paleontol. 71 (3), 525–527.
Kellner, A.W., Moody, J.M., 2003. Pterosaur (Pteranodontoidea, Pterodactyloidea) scapulocoracoid from the early Cretaceous of Venezuela:. Geol. Soc. Lond. Spec. 217 (1), 73–77.
Kellner, A.W., Tomida, Y., 2000. Description of a new species of Anhangueridae (Pterodactyloidea) with comments on the pterosaur fauna from the Santana Formation (Aptian-Albian), northeastern Brazil: Natl. Sci. Mus. Monogr. 17, ix–137.
Kellner, A.W., Rich, T.H., Costa, F.R., Vickers-Rich, P., Kear, B.P., Walters, M., Kool, L., 2010. New isolated pterodactyloid bones from the Albian Toolebuc Formation (western Queensland, Australia) with comments on the Australian pterosaur fauna. Alcheringa 34 (3), 219–230.
Kellner, A.W., Rodrigues, T., Costa, F.R., 2011. Short note on a pteranodontoid pterosaur (Pterodactyloidea) from western Queensland, Australia. An. Acad. Bras. Cienc. 83 (1), 301–308.
Kellner, A.W., Holgado, B., Grillo, O., Pretto, F.A., Kerber, L., Pinheiro, F.L., Soares, M. B., Schultz, C.L., Lopes, R.T., Araújo, O., 2022. Reassessment of *Faxinalipterus minimus*, a purported Triassic pterosaur from southern Brazil with the description of a new taxon. PeerJ 10, e13276.
Kellner, A.W.A., Weinschütz, L.C., Holgado, B., Bantim, R.A.M., Sayão, J.M., 2019c. A new toothless pterosaur (Pterodactyloidea) from Southern Brazil with insights into the paleoecology of a Cretaceous desert. An. Acad. Bras. Cienc. v, 91.
Kellner, A. W. A., 2003b, Comments on the phylogeny of the Pterodactyloidea: Rivista del Museo Civico di Scienze Naturali "E. Caffi" di Bergamo, v. 22, p. 31–37.
Kellner, A., 2004, Chapter 2: The Ankle Structure of Two Pterodactyloid Pterosaurs from the Santana Formation (Lower Cretaceous), Brazil: Bull. Am. Mus. Nat. Hist., p. 25-35.
Kellner, A. W., 2010, Comments on the Pteranodontidae (Pterosauria, Pterodactyloidea) with the description of two new species: Anais da Academia Brasileira de Ciências, v. 82, no. 4, p. 1063-1084.
Knoll, F., Pterosaurs from the Lower Cretaceous (? Berriasian) of Anoual, Morocco, *in* Proceedings Annales de Paléontologie 2000, Volume 86, Elsevier, p. 157-164.
Kozur, H.W., Weems, R.E., 2010. The biostratigraphic importance of conchostracans in the continental Triassic of the northern hemisphere: Geol. Soc. Lond. Spec. 334 (1), 315–417.
Labita, C., Martill, D.M., 2021. An articulated pterosaur wing from the Upper Cretaceous (Maastrichtian) phosphates of Morocco:Cretac. Res. 119,104679.
Lawson, D.A., 1975. Pterosaur from the latest Cretaceous of West Texas: discovery of the largest flying creature. Science 187 (4180), 947–948.
Leal, M.E.C., Pêgas, R.V., Bonde, N., Kellner, 2017. Cervical vertebrae of an enigmatic pterosaur from the Crato Formation (Lower Cretaceous, Araripe Basin, NE Brazil). Geol. Soc. Lond. Spec. 455 (1), 195–208.
Leanza, H., Zeiss, A., 1992. On the ammonite fauna of the Lithographic Limestones from the Zapala region (Neuquén province, Argentina), with the description of a new genus. Zbl. Geol. Paläontol. 1991 (6), 1841–1850.
Leonardi, G., Borgomanero, G., 1983. *Cearadactylus atrox* nov. gen., nov. sp.: novo pterosauria (Pterodactyloidea) da Chapada do Araripe, Ceara, Brasil, *in*. Proceedings 7° Congresso Brasileiro de Paleontologia 17.
Leonardi, G., Borgomanero, G., 1985. *Cearadactylus atrox* nov. gen., nov. sp., novo pterosauria (Pterodactyloidea) da Chapada do Araripe, Ceará, Brasil: Coletâ nea de Trabalhos Paleontolo gicos, Se rie Geologia. Brasilia v. 27, 75–80.
Lewy, Z., Milner, A.C., Patterson, C., 1992. Remarkably preserved natural endocranial casts of pterosaur and fish from the Late Cretaceous of Israel: Geological Survey of Israel. Current Research 7, 31–35.
Lkebir, N., Masrour, M., Pascual-Arribas, C., de Ducla, M., Hernandez-Medrano, N., and Pérez-Lorente, F., 2020a, Short report: The Anza tracksite: Ichnological heritage and geoeducational significance of dinosaur and pterosaur tracks in coastal Morocco: J. Afr. Earth Sci, p. 103949.
Lkebir, N., Masrour, M., Pascual-Arribas, C., de Ducla, M., Hernández-Medrano, N., Pérez-Lorente, F., 2020b. The Anza tracksite: Ichnological heritage and geoeducational significance of dinosaur and pterosaur tracks in coastal Morocco. J. Afr. Earth Sci 171, 103949.
Longrich, N.R., Martill, D.M., Andres, B., 2018. Late Maastrichtian pterosaurs from North Africa and mass extinction of Pterosauria at the Cretaceous-Paleogene boundary. PLoS Biol. 16 (3), e2001663.
Lü, J., and Ji, Q., 2005, New azhdarchid pterosaur from the Early Cretaceous of western Liaoning: Acta Geologica Sinica (English Edition), v. 79, no. 3, p. 301-307.
Lü, J., and Zhang, B., 2005, New pterodactyloid pterosaur from the Yixian Formation of Western Liaoning: Dizhi Lunping(Geol. Rev.), v. 51, no. 4, p. 458-462.
Lü, J., Ji, S. a., Yuan, C., Gao, Y., Sun, Z., and Ji, Q., New pterodactyloid pterosaur from the Lower Cretaceous Yixian Formation of western Liaoning, *in* Proceedings Papers from the 2005 Heyuan International Dinosaur Symposium. Beijing: Geological Publishing House2006b, p. P195-203.
Lü, J., Meng, Q., Wang, B., Liu, D., Caizhi, S., Yuguang, Z., 2018. In: Hone, D.W.E., Witton, M.P., Martill, D.M. (Eds.), New Perspectives on Pterosaur Palaeobiology, 455. Geological Society, London, pp. 95–104.
Lü, J., Fucha, X., 2010. A new pterosaur (Pterosauria) from Middle Jurassic Tiaojishan formation of western Liaoning, China:. Glob. Geol. 13, 113–118.

Lü, J., Gao, C., Liu, J., Meng, Q., Ji, Q., 2006a. New material of the pterosaur *Eopteranodon* from the Early Cretaceous Yixian Formation, western Liaoning, China: Geol. Bull. China 25 (5), 565–571.
Lü, J., Gao, Y., Xing, L., Li, Z., Ji, Q., 2007. A new species of *Huaxiapterus* (Pterosauria: Tapejaridae) from the Early Cretaceous of western Liaoning, China. Acta Geol. Sin. 81 (5), 683–687.
Lü, J., Unwin, D.M., Xu, L., Zhang, X., 2008. A new azhdarchoid pterosaur from the Lower Cretaceous of China and its implications for pterosaur phylogeny and evolution. Naturwissenschaften 95 (9), 891–897.
Lü, J., Azuma, Y., Dong, Z., Barsbold, R., Kobayashi, Y., Lee, Y.N., 2009. New material of dsungaripterid pterosaurs (Pterosauria: Pterodactyloidea) from western Mongolia and its palaeoecological implications:. Geol. Mag. 146 (5), 690–700.
Lü, J., Fucha, X.H., Chen, J.M., 2010a. A new scaphognathine pterosaur from the Middle Jurassic of western Liaoning, China. Diqiu Xuebao(Acta Geoscientica Sinica) 31 (2), 263–266.
Lü, J., Unwin, D.M., Jin, X., Liu, Y., Ji, Q., 2010b. Evidence for modular evolution in a long-tailed pterosaur with a pterodactyloid skull: Proc. R. Soc. Lond. B: Biol. Sci. 277 (1680), 383–389.
Lü, J., Unwin, D.M., Deeming, D.C., Jin, X., Liu, Y., Ji, Q., 2011. An egg-adult association, gender, and reproduction in pterosaurs. Science 331 (6015), 321–324.
Lü, J., Unwin, D.M., Zhao, B., Gao, C., Shen, C., 2012. A new rhamphorhynchid (Pterosauria: Rhamphorhynchidae) from the Middle/Upper Jurassic of Qinglong, Hebei Province, China:. Zootaxa 3158 (1), 1–19.
Mader, B.J., Kellner, A.W.A., 1999. A new anhanguerid pterosaur from the Cretaceous of Morocco: Boletim do Museu Nacional. Rio de Janeiro, Nova Serie, Geologia 45, 1–11.
Malkani, M.S., 2020. Theropods, Mesoeucrocodiles and Pterosaurs Found from the Latest Maastrichtian Vitakri Formation of Balochistan, Pakistan; Description with Large Photographs and Comparison with Coeval Taxa from Indo-Pakistan Subcontinent:. Open J. Geol. 10 (05), 510.
Malkani, M.S., 2021. Formal Description of Mesozoic and Cenozoic Biotas Found from Pakistan:. Open J. Geol. 11 (9), 411–455.
Malkani, M., 2013 New pterosaur from the latest Cretaceous terrestrial strata of Pakistan, *in* Proceedings Abstract Book of 9th International Symposium on the Cretaceous System, September 1–5.
Malkani, M. S., 2018, Rapid discoveries of giant pes and associated manus footprints and tracks of titanosaurian sauropods from Pakistan: a review of Mesozoic ichnites from Indo-Pak subcontinent. 1–71p: Researchgate. net, Research, DOI, v. 10.
Malkani, M. S., 2019, Pterosaurs from Indo-Pakistan subcontinent; Were Cretaceous pterosaurs tooth bearing? Diagnostic features of *Saraikisaurus minhui* a toothed, youngest and latest Cretaceous pterosaur.
Manzig, P.C., Kellner, A.W., Weinschütz, L.C., Fragoso, C.E., Vega, C.S., Guimarães, G. B., Godoy, L.C., Liccardo, A., Ricetti, J.H., de Moura, C.C., 2014. Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles. PLoS One 9 (8), e100005.
Marsh, O.C., 1872. Discovery of additional remains of Pterosauria with descriptions of two new species. Am. J. Sci. 3 (16), 241–248.
Martill, D.M., 1993. Fossils of the Santana and Crato formations. Brazil 5, 159.
Martill, D.M., 2008. First pterosaur remains from the Exu Formation (Cretaceous) of the Araripe Basin, Brazil. Zitteliana, pp. 243–248.
Martill, D.M., 2011. A new pterodactyloid pterosaur from the Santana Formation (Cretaceous) of Brazil:. Cretac. Res. 32 (2), 236–243.
Martill, D.M., and Ibrahim, N., 2015, An unusual modification of the jaws in cf. *Alanqa*, a mid-Cretaceous azhdarchid pterosaur from the Kem Kem beds of Morocco: Cretaceous Research, v. 53, p. 59–67.
Martill, D.M., Moser, M., 2018. Topotype specimens probably attributable to the giant azhdarchid pterosaur *Arambourgiania philadelphiae* (Arambourg 1959). Geol. Soc. Lond. Spec. 455, SP455.–456.
Martill, D.M., Brito, P. M., Wenz, S., and Wilby, P. R., 1993, Fossils of the Santana and Crato formations, Brazil, Palaeontological Association.
Martill, D.M., Frey, E., 1998. A new pterosaur lagerstatte in NE Brazil (Crato Formation; Aptian, Lower Cretaceous): preliminary observations. Oryctos 1, 79–85.
Martill, D., Frey, E., Diaz, G.C., Bell, C., 2000. Reinterpretation of a Chilean pterosaur and the occurrence of Dsungaripteridae in South America:. Geol. Mag. 137 (1), 19–25.
Martill, D.M., Heimhofer, U., 2007. Stratigraphy of the Crato Formation. In: Martill, D., Bechly, G., Loveridge, R. (Eds.), The Crato fossil beds of Brazil: Window into an ancient world: Cambridge. Cambridge University Press, pp. 25–43.
Martill, D.M., Naish, D., 2006. Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. Palaeontology 49 (4), 925–941.
Martill, D.M., Smith, R., Unwin, D.M., Kao, A., McPhee, J., Ibrahim, N., 2020b. A new tapejarid (Pterosauria, Azhdarchoidea) from the mid-Cretaceous Kem Kem beds of Takmout, southern Morocco: Cretac. Res. 112, 104424.
Martill, D.M., Unwin, D.M., 1989. Exceptionally well preserved pterosaur wing membrane from the Cretaceous of Brazil. Nature 340 (6229), 138–140.
Martill, D.M., Frey, E., Bell, C., Diaz, G.C., 2006. Ctenochasmatid pterosaurs from Early Cretaceous deposits in Chile: Cretac. Res. 27 (5), 603–610.
Martill, D.M., Ibrahim, N., Bouaziz, S., 2018a. A giant pterosaur in the Early Cretaceous (Albian) of Tunisia. J. Afr. Earth Sci. 147, 331–337.
Martill, D. M., Unwin, D. M., Ibrahim, N., and Longrich, N., 2018b, A new edentulous pterosaur from the Cretaceous Kem Kem beds of south eastern Morocco: Cretac. Res., 84, 1–12.
Martill, D.M., Green, M., Smith, R.E., Jacobs, M.L., Winch, J., 2020a. First tapejarid pterosaur from the Wessex Formation (Wealden Group: Lower Cretaceous, Barremian) of the United Kingdom: Cretac. Res. 113, 104487.
Soares, M., Dalla Vecchia, F., Schultz, C., Kellner, A., 2013. On the supposed pterosaurian nature of *Faxinalipterus minima* Bonaparte et al. (2010) from the Upper Triassic of Rio Grande do Sul, Brazil, *in* Proceedings International Symposium on Pterosaurs, Short Comunications, rio de Janeiro. Universidade Federal do Rio de Janeiro, Museu. 95–98.
Martill, D. M., 1988, Preservation of Fish in the Cretaceous Santana Formation of Brazil.
Martin, J.E., Broin F, D.L.D., 2016. A miniature notosuchian with multicuspid teeth from the Cretaceous of Morocco. J. Vertebr. Paleontol. 36 (6), e1211534.
Martinelli, A.G., Garrido, A.C., Forasiepi, A.M., Paz, E.R., Gurovich, Y., 2007. Notes on fossil remains from the early cretaceous Lohan Cura formation, Neuquén Province, Argentina. Gondwana Res. 11 (4), 537–552.
Martínez, R.N., Apaldetti, C., Correa, G., Colombi, C.E., Fernández, E., Malnis, P.S., Praderio, A., Abelín, D., Benegas, L.G., Aguilar-Cameo, A., Alcober, O.A., 2015b. A new Late Triassic vertebrate assemblage from northwestern Argentina. Ameghiniana 52 (4), 379–390.
Martínez, R.N., Andres, B., Apaldetti, C., Cerda, I.A., 2022. The dawn of the flying reptiles: first Triassic record in the southern hemisphere. Pap. 8 (2), e1424.
Martínez, F., Peña, M., Arriagada, C., 2015a. Servicio Nacional de Geología y Minería, Carta Geológica de Chile, Serie Geología Básica. Escala 1 (100), 179–180.
Martin-Silverstone, E., Unwin, D.M., Cuff, A.R., Brown, E.E., Allington-Jones, L., Barrett, 2022. A new pterosaur from Skye, Scotland and the early diversification of flying reptiles. bioRxiv.
Masrour, M., de Ducla, M., Billon-Bruyat, J.P., Mazin, 2018. Rediscovery of the Tagragra Tracksite (Maastrichtian, Agadir, Morocco): *Agadirichnus elegans* Ambroggi and Lapparent 1954 is Pterosaurian Ichnotaxon. Ichnos 25 (4), 285–294.
Masrour, M., Pascual-Arribas, C., de Ducla, M., Hernández-Medrano, N., Pérez-Lorente, F., 2017. Anza palaeoichnological site. Late Cretaceous. Morocco. Part I. The first African pterosaur trackway (manus only). J. Afr. Earth Sci.134, 766–775.
Mateus, O., Polcyn, M. J., Jacobs, L. L., Araújo, R., Schulp, A. S., Marinheiro, J., Pereira, B., and Vineyard, D., 2012, Cretaceous amniotes from Angola: dinosaurs, pterosaurs, mosasaurs, plesiosaurs, and turtles: V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno.
Mawson, J., Smith Woodward, A., 1907. On the Cretaceous formation of Bahia (Brazil), and on vertebrate fossils collected therein:. Q. J. Geol. Soc. 63 (1–4), pp. 128-NP.
McPhee, J., Ibrahim, N., Kao, A., Unwin, D.M., Smith, R., Martill, 2020. A new? chaoyangopterid (Pterosauria: Pterodactyloidea) from the Cretaceous Kem Kem beds of Southern Morocco. Cretac. Res. 110, 104410.
Melo, R. M., Guzmán, J., Almeida-Lima, D., Piovesan, E. K., and Neumann, V. H. d. M. L., 2020, New marine data and age accuracy of the Romualdo Formation, Araripe Basin, Brazil: Sci. Rep., v. 10, no. 1, p. 1-15.
Molnar, R., 1987. A pterosaur pelvis from western Queensland, Australia. Alcheringa 11 (2), 87–94.
Molnar, R., Thulborn, R., 1980. First pterosaur from Australia. Nature v. 288 (5789), 361–363.
Molnar, R.E., Thulborn, R.A., 2007. An incomplete pterosaur skull from the Cretaceous of north-central Queensland, Australia:. Arquivos do Museu Nacional Rio de Janeiro 65, 461–470.
Molnar, R., Wiffen, J., 1994. A Late Cretaceous polar dinosaur fauna from New Zealand:. Cretac. Res. 15 (6), 689–706.
Montanelli, S.B., 1987. Presencia de Pterosauria (Reptilia) en la Formación La Amarga (Hauteriviano-Barremiano), Neuquén, Argentina:. Ameghiniana 24 (1–2), 109–113.
Monteillet, J., Lappartient, J., and Taquet, P., 1982, Un Ptérosaurien géant dans le Crétacé supérieur de Paki (Sénégal): Comptes rendus de l'Académie des sciences. Série 2. Fascicule a, Sciences de la terre et des planètes= Earth and planetary sciences, v. 295, p. 409.
Mourgues, F.A., 2004. Advances in ammonite biostratigraphy of the marine Atacama basin (Lower Cretaceous), northern Chile, and its relationship with the Neuquén basin, Argentina. J. S. Am. Earth Sci. 17 (1), 3–10.
Myers, T.S., 2010. A new ornithocheirid pterosaur from the Upper Cretaceous (Cenomanian–Turonian) Eagle Ford Group of Texas. J. Vertebr. Paleontol. 30 (1), 280–287.
Nesbitt, S.J., 2009. The early evolution of archosaurs: relationships and the origin of major clades. Columbia University.
Nesov, L., Kanznyshkina, L., Cherepanov, G., 1987. Dinosaurs, crocodiles and other archosaurs from the Late mesozoic of central Asia and their place in ecosystems: Abstracts of the 33rd session of the All Union Palaeontological Society. Leningrad, 46–47.
Novas, F.E., Kundrat, M., Agnolín, F.L., Ezcurra, M.D., Ahlberg, P.E., Isasi, M.P., Arriagada, A., Chafrat, P., 2012. A new large pterosaur from the Late Cretaceous of Patagonia. J. Vertebr. Paleontol. 32 (6), 1447–1452.
Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.I., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: the evidence from Patagonia: Cretac. Res. 45, 174–215.
Ntamak-Nida, M.J., Ketchemen-Tandia, B., Ewane, R.V., Lissock, J.P., Courville, P., 2006. Nouvelles données sur les Mollusques et autres macro-organismes campaniens de Sikoum (Centre-Est du sous basin de Douala-Cameroun): intérêts bio-chronologiques et paléo-écologiques. Afr. Geosci. Rev. 13 (3/4), 385–394.

Nuvens, P. C., Sayão, J. M., Silva, H., Saraiva, A., and Kellner, A. W., 2002, A coleção de pterossauros do Museu de Paleontologia de Santana do Cariri, Nordeste do Brasil: Arquivos do Museu Nacional, Rio de Ja– neiro, v. 60, p. 235-240.
O'Connor, P.M., Sertich, J.J., Manthi, F.K., 2011. A pterodactyloid pterosaur from the Upper Cretaceous Lapurr sandstone, West Turkana, Kenya. Anais da Academia Brasileira de Ciências 83 (1), 309–315.
Ortiz David, L.D., Riga, B.J.G., Kellner, A.W., 2022. *Thanatosdrakon amaru*, gen. et sp. nov., a giant azhdarchid pterosaur from the upper Cretaceous of Argentina. Cretac. Res. 105228
Ortiz, David, González Riga, B.J., Kellner, A.W.A., 2017. Discovery of the largest pterosaur from South America. Cretac 83, 40–46.
Ostrom, J.H., 1978. The osteology of *Compsognathus longipes* Wagner. Zitteliana.
Padian, K., 1985. The origins and aerodynamics of flight in extinct vertebrates. Palaeontology 28 (3), 413–433.
Padian, K., 2004. The nomenclature of Pterosauria (Reptilia, Archosauria). Proceedings First International Phylogenetic Nomenclature Meeting. Muséum National d'Histoire Naturelle Volume 27.
Padian, K., 2008a. The Early Jurassic pterosaur *Campylognathoides* Strand. Spec. Pap. Palaeontol. 80, 65–107.
Padian, K., 2008b. 2008b, The Toarcian (Early Jurassic) pterosaur *Dorygnathus* Wagner. Palaeontology 80, 1–64.
Parkinson, J., 1930, The dinosaur in East Africa. An account of the giant reptile beds of Tendaguru, Tanganyika Territory., HF & G. Witherby.
Pêgas, R.V., de Castro Leal, M.E., Kellner, A.W.A., 2016. A Basal Tapejarine (Pterosauria; Pterodactyloidea; Tapejaridae) from the Crato Formation, Early Cretaceous of Brazil. PloS one 11 (9), e0162692.
Pêgas, R.V., Costa, F.R., Kellner, A.W.A., 2018. New Information on the osteology and a taxonomic revision of the genus *Thalassodromeus* (Pterodactyloidea, Tapejaridae, Thalassodrominae). J. Vertebr. Paleontol. 38 (2), e1443273.
Pêgas, R.V., Holgado, B., Leal, 2019. On *Targaryendraco wiedenrothi* gen. nov. (Pterodactyloidea, Pteranodontoidea, Lanceodontia) and recognition of a new cosmopolitan lineage of Cretaceous toothed pterodactyloids:. Hist. Biol. 33 (8), 1266–1280.
Pentland, A. H., Poropat, S. F., White, M. A., Rigby, S. L., Vickers-Rich, P., Rich, T. H., and Elliott, D. A., 2022b, New anhanguerian pterosaur remains from the Lower Cretaceous of Queensland, Australia: Alcheringa: An Australasian Journal of Palaeontology, 46(2), 188–197.
Pentland, A.H., Poropat, S.F., 2019. Reappraisal of *Mythunga camara* Molnar & Thulborn, 2007 (Pterosauria, Pterodactyloidea, Anhangueria) from the upper Albian Toolebuc Formation of Queensland, Australia:. Cretac. Res. 93, 151–169.
Pentland, A.H., Poropat, S.F., Tischler, T.R., Sloan, T., Elliott, R.A., Elliott, H.A., Elliott, J. A., Elliott, D.A., 2019. *Ferrodraco lentoni* gen. et sp. nov., a new ornithocheirid pterosaur from the Winton Formation (Cenomanian–lower Turonian) of Queensland, Australia. : Sci. Rep. 9 (1), 13454.
Pentland, A. H., Poropat, S. F., White, M. A., Rigby, S. L., Bevitt, J. J., Duncan, R. J., Sloan, T., Elliott, R. A., Elliott, H. A., Elliott, J. A., and Elliott, D. A., 2022a, The osteology of *Ferrodraco lentoni*, an anhanguerid pterosaur from the mid-Cretaceous of Australia: J. Vertebr. Paleontol., 41(5), e2038182.
Perea, D., Soto, M., Veroslavsky, G., Martínez, S., Ubilla, M., 2009. A Late Jurassic fossil assemblage in Gondwana: biostratigraphy and correlations of the Tacuarembó Formation, Parana Basin, Uruguay. J. S. Am. Earth Sci. 28 (2), 168–179.
Perea, D., Soto, M., Toriño, P., Mesa, V., Maisey, J.G., 2018. A Late Jurassic-?earliest Cretaceous ctenochasmatid (Pterosauria, Pterodactyloidea): The first report of pterosaurs from Uruguay. J. S. Am. Earth 85, 298–306.
Pereda Suberbiola, X., Bardet, N., Jouve, S., Iarochène, M., Bouya, B., Amaghzaz, M., 2003. A new azhdarchid pterosaur from the Late Cretaceous phosphates of Morocco:. Geol. Soc. Lond. Spec. 217 (1), 79–90.
Philip, J., Bellion, Y., Babinot, J. F., Tronchetti, G., Fourcade, E., Ricou, L. E., Guiraud, R., Bellion, Y., Herbin, J. P., Combes, P. J., Cornee, J. J., Dercourt, J., 1993. Late Cenomanian (94 to 92 Ma), in: Dercourt, J., Ricou, L. E., and Vrielynck, B., eds., Atlas Tethys palaeoenvironmental maps: Gauthier Villars, Paris, pp. 153–178.
Pinheiro, F.L., Rodrigues, T., 2017. *Anhanguera* taxonomy revisited: is our understanding of Santana Group pterosaur diversity biased by poor biological and stratigraphic control? PeerJ 5, e3285.
Pinheiro, F.L., Horn, B.L., Schultz, C.L., de Andrade, J.A., Sucerquia, P.A., 2012. Fossilized bacteria in a Cretaceous pterosaur headcrest. Lethaia 45 (4), 495–499.
Pinheiro, F.L., Prado, G., Ito, S., Simon, J.D., Wakamatsu, K., Anelli, L.E., Andrade, J.A.F., Glass, K., 2019. Chemical characterization of pterosaur melanin challenges color inferences in extinct animals: Sci. Rep. 9 (1), 15947.
Pinheiro, F.L., Schultz, C.L., 2012. An unusual pterosaur specimen (Pterodactyloidea,? Azhdarchoidea) from the Early Cretaceous Romualdo Formation of Brazil, and the evolution of the pterodactyloid palate. PLoS One 7 (11), e50088.
Polcyn, M.J., Tchernov, E., Jacobs, L.L., 1999. The Cretaceous biogeography of the eastern Mediterranean with a description of a new basal mosasauroid from'Ein Yabrud, Israel:. Natl. Sci. Mus. Monogr. 15, 259–290.
Pons, D., Berthou, P., and Campos, D. d. A., 1990, Quelques observations sur la palynologie de l'Aptien Supérieur et de l'Albien du Bassin d'Araripe (NE du Brésil): Atas do, v. 1, p. 241-252.
Poropat, S.F., Martin, S.K., Tosolini, A.M.P., Wagstaff, B.E., Bean, L.B., Kear, B.P., Vickers-Rich, P., Rich, T.H., 2018. Early Cretaceous polar biotas of Victoria, southeastern Australia—an overview of research to date. Alcheringa: An Australasian Journal of Palaeontology 42, 157–229.
Prasad, G., and Manhas, B., 2007, A new docodont mammal from the Jurassic Kota Formation of India: Palaeontol. Electron., v. 10, no. 2, p. 1-11.
Price, L., 1953. A presença de Pterosauria no Cretáceo Superior do Estado da Paraíba. Notas Preliminares e Estudos, Divisao de Geologia e Mineralogia, Brasil 71, 1–10.
Price, L., 1971. A presenca de Pterosauria no Cretaceo inferior da Chapada do Araripe, Brasil. An. Acad. Bras. Cienc. v. 43(Supplement), 452-461.
Prondvai, E., Stein, K., Ősi, A., Sander, M.P., 2012. Life history of *Rhamphorhynchus* inferred from bone histology and the diversity of pterosaurian growth strategies. PLoS One 7 (2), e31392.
Raja, N.B., Dunne, E.M., Matiwane, A., Khan, T.M., Nätscher, P.S., Ghilardi, A.M., Chattopadhyay, D., 2021. Colonial history and global economics distort our understanding of deep-time biodiversity:Nat. Ecol. Evol. 2 (6), 145–154.
Rao, C.N., Shah, S.C., 1963. On the occurrence of pterosaur from the Kota-Maleri beds of Chanda District, Maharashtra:. Rec. GSI. 92, 315–318.
Rauhut, O., Puerta, P., 2001. New vertebrate fossils from the middle-late Jurassic Canadón Asfalto formation of chubut, Argentina. Ameghiniana 38 (4), 16.
Reck, H., 1931. Die deutschostafrikanischen Flugsaurier (*Pterodactylus brancai* [Tendaguripterus]): Centralblatt für Mineralogie. Geologie und Paläontologie 1931, 321–336.
Rich, T. H., and Vickers-Rich, P., 2020, Dinosaurs of Darkness: In Search of the Lost Polar World, Indiana University Press.
Rich, T.H., Rich, P.V., 1989. Polar dinosaurs and biotas of the Early Cretaceous of southeastern Australia: Nat. Geog. Res. 5 (1), 15–53.
Rich, T.H., Vickers-Rich, P., 2000. Dinosaurs of Darkness. Indiana University Press, Indiana.
Richards, T.M., Stumkat, P.E., Salisbury, 2021. A new species of crested pterosaur (Pterodactyloidea, Anhangueridae) from the Lower Cretaceous (upper Albian) of Richmond, North West Queensland. Australia: J. Vertebr. Paleontol. 41 (3), e1946068.
Roberts, E., Jelsma, H. A., and Hegna, T., 2015, Mesozoic sedimentary cover sequences of the Congo Basin in the Kasai Region, Democratic Republic of Congo, Geology and Resource Potential of the Congo Basin, Springer, p. 163–191.
Rodrigues, T., Kellner, A. W., Mader, B. J., and Russell, D. A., 2011, New pterosaur specimens from the Kem Kem beds (Upper Cretaceous, Cenomanian) of Morocco: Rivista Italiana di Paleontologia e Stratigrafia (Research In Paleontology and Stratigraphy), v. 117, no. 1.
Rodrigues, T., Kellner, 2008. Review of the pterodactyloid pterosaur *Coloborhynchus*. Zitteliana, 219–228.
Rodrigues, T., Kellner, A.W.A., 2010. Note on the pterosaur material described by Woodward from the Recôncavo Basin, Lower Cretaceous, Brazil:. Rev. Bras. de Pal. 13 (2), 159–164.
Rodrigues, T., Kellner, A.W.A., 2013. Taxonomic review of the *Ornithocheirus* complex (Pterosauria) from the Cretaceous of England. ZooKeys 308, 1–112.
Ronda, G., Ghiglione, M. C., Martinod, J., Barberón, V., Ramos, M. E., Coutand, I., Grujic, D., and Kislitsyn, R., 2022, Early Cretaceous to Cenozoic Growth of the Patagonian Andes as Revealed by Low-Temperature Thermochronology: Tectonics, v. 41, no. 10, p. e2021TC007113.
Rosenbach, K., Zalmout, I., Wilson, J.A., 2018. Three-dimensionally preserved pterosaur material from the Late Cretaceous of Afro-Arabia provides insight into pterosaur flight, in: Proceedings 5th International Paleontological Congress, Paris, 2018.
Rubilar, D., Vargas, A., Kellner, A.W., 2002. Vértebras cervicales de Pterodactyloidea (Archosauria, Pterosauria) de la Formación Quebrada Monardes (Cretácico Inferior), norte de Chile. Ameghiniana 39, 16R–17R.
Saint-Marc, P., 1978. Arabian peninsula: The Phanerozoic geology of the world II: The Mesozoic: Amsterdam. Elsevier, 435–462.
Salinas, P., Marshall, L., Sepúlveda, P., 1991. Vertebrados continentales del Paleozoico y Mesozoico de Chile, *in*. Proceedings Congreso geologico chileno 6, 310–313.
Sanchez, T.M., 1973. Redescripción del cráneo y mandíbulas de *Pterodaustro guiñazui* Bonaparte (Pterodactyloidea, Pterodaustriidae). Ameghiniana 10 (4), 313–325.
Sayão, J. M., and Kellner, A. W. A., Comments on Pterosaur fauna from Tendaguru, Upper Jurassic of Africa, with the identification of a possible Azhdarchid, *in* Proceedings Acre: Universidade Federal do Acre2001b, p. 145.
Sayão, J., Kellner, A., 1998. Pterosaur wing with soft tissue from the Crato Member (Aptian-Albian), Santana Formation, Brazil. J. Vertebr. Paleontol. 18 (3), 75A.
Sayão, J.M., Kellner, A.W.A., 2000. Description of a Pterosaur Rostrum from the Crato Member, Santana Formation (Aptian-Albian), Northeastern, Brazil.
Sayão, J.M., Kellner, A.W.A., 2001a. New data on the pterosaur fauna from Tendaguru (Tanzania), Upper Jurassic, Africa. J. Vertebr. Paleontol. v. 21, no. 3 (Supplementary), 97A.
Scasso, R., Concheyro, A., 1999. Nanofósiles calcáreos, duración y origen de ciclos caliza-marga (Jurásico tardío de la Cuenca Neuquina). Rev. Asoc. Geol. Argent. 54 ((3),), 290–297.
Sereno, P.C., Brusatte, S.L., 2008. Basal abelisaurid and carcharodontosaurid theropods from the Lower Cretaceous Elrhaz Formation of Niger:. Acta Palaeontol. Pol. 53 (1), 15–46.
Sigogneau-Russell, D., Evans, S., Levine, J., and Russell, D., 1998, The Early Cretaceous microvertebrate locality of Anoual, Morocco: a glimpse at the small vertebrate assemblages of Africa: New Mex. Mus. Nat. Hist. Sci Bull., v. 14, p. 177-181.
Smith, R. E., Ibrahim, N., Longrich, N., Unwin, D. M., Jacobs, M. L., Williams, C. J., Zouhri, S., and Martill, D. M., 2022, The pterosaurs of the Cretaceous Kem Kem Group of Morocco: PalZ, p. 1-53.

Smith, N.D., Makovicky, P.J., Agnolin, F.L., Ezcurra, M.D., Pais, D.F., Salisbury, S.W., 2008. A *Megaraptor*-like theropod (Dinosauria: Tetanurae) in Australia: support for faunal exchange across eastern and western Gondwana in the Mid-Cretaceous: Proc. R. Soc. Lond. B: Biol. Sci. 275 (1647), 2085–2093.
Smith, R. E., Martill, D. M., Kao, A., Zouhri, S., and Longrich, N., 2020, A long-billed, possible probe-feeding pterosaur (Pterodactyloidea: ?Azhdarchoidea) from the mid-Cretaceous of Morocco, North Africa: Cretac. Res, North Africa 118, 104643.
Smith, E., Smith, R., 1999. Black Opal Fossils of Lighting Ridge: Treasures from the Rainbow Billabong. Kangaroo Press.
Sömmering, S.T., 1812. Über einen Ornithocephalus oder über das unbekannten Thier der Vorwelt, dessen Fossiles Gerippe Collini im 5. Bande der Actorum Academiae Theodoro-Palatinae nebst einer Abbildung in natürlicher Grösse im Jahre 1784 beschrieb, und welches Gerippe sich gegenwärtig in der Naturalien-Sammlung der königlichen Akademie der Wissenschaften zu München befindet: Denkschriften der Akademie der Wissenschaften München. Mathematisch-Physik 3, 89–158.
Soto, M., Montenegro, F., Toriño, P., Mesa, V., Perea, D., 2021. A new ctenochasmatid (Pterosauria, Pterodactyloidea) from the late Jurassic of Uruguay. J. S. Am. Earth Sci. 111, 103472.
Steel, L., 2003. The John Quekett sections and the earliest pterosaur histological studies:. Geol. Soc. Lond. Spec. 217 (1), 325–334.
Steel, L., Martill, D.M., Unwin, D.M., Winch, J.D., 2005. A new pterodactyloid pterosaur from the Wessex Formation (Lower Cretaceous) of the Isle of Wight, England:. Cretac. Res. 26 (4), 686–698.
Steel, L., 2008, The palaeohistology of pterosaur bone: an overview: Zitteliana, p. 109-125.
Swinton, W.E., 1948. A Cretaceous pterosaur from the Belgian Congo. Bulletin de la Société Belge de Géologie de Paléontologie et d'Hydrologie 77, 234.
Traub, D., Archer, M., Hand, S., and Godthelp, H., 2017, Review of the Early Cretaceous Hazel Creek assemblage, the oldest mammal-bearing fauna in northern Australia, CAVEPS 2017: 16th Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, Queenstown, 3rd–5th October 2017.: Queenstown, New Zealand.
Unwin, D.M., 2001. An overview of the pterosaur assemblage from the Cambridge Greensand (Cretaceous) of Eastern England:. Foss. Rec. 4 (1), 189–221.
Unwin, D., 2002. On the systematic relationships of *Cearadactylus atrox*, an enigmatic Early Cretaceous pterosaur from the Santana Formation of Brazil:. Foss. Rec. 5 (1), 239–263.
Unwin, D., 2003. On the phylogeny and evolutionary history of pterosaurs:. Geol. Soc. Lond. Spec. 217 (1), 139–190.
Unwin, D., 2005. The pterosaurs from deep time. Pi Press, New York.
Unwin, D., Rauhut, O., Haluza, A., 2004. The first "Rhamphorhynchoid" from South America and the early history of pterosaurs Göttingen. Germany: Geobiologie 74, 235–237.
Unwin, D.M., Heinrich, W.D., 1999. On a pterosaur jaw from the Upper Jurassic of Tendaguru (Tanzania):. Foss. Rec. 2 (1), 121–134.
Unwin, D.M., Lü, J., 1997. On *Zhejiangopterus* and the relationships of pterodactyloid pterosaurs: Hist. Biol. 12 (3–4), 199–210.
Unwin, D., Martill, D., 2007. Pterosaurs of the Crato Formation. Window into an ancient world, Cambridge University Press, The Crato fossil beds of Brazil, pp. 475–524.
Unwin, D., Preliminary results of a phylogenetic analysis of the Pterosauria (Diapsida: Archosauria), *in* Proceedings Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota1995, China Ocean Press Beijing, p. 69–72.
Unwin, D., 1996, The fossil record of Middle Jurassic pterosaurs: Museum of Northern Arizona Bulletin, v. 60, p. 291-304.
Upchurch, P., Andres, B., Butler, R.J., Barrett, P.M., 2015. An analysis of pterosaurian biogeography: implications for the evolutionary history and fossil record quality of the first flying vertebrates. Hist. Biol. 27 (6), 697–717.
Neumann, L., Mabesoone, V.H., 2003. An overview on Callovian-Cenomanian intracratonic basins of Northeast Brazil: Onshore stratrigraphic record of the opening of the southern Atlantic. Geologica Acta: an international earth science journal 1 (3), 261–276.
van Dijk, D., 1978. Trackways in the Stormberg:. Palaeontol. Afr. 21, 113–120.
Van Dijk, D.E., 2001. Jurassic bipeds that could hop? perch? pounce? fly?: news & views:. S. Afr. J. Sci. 97 (9), 373–374.
van Dijk, D.E., Eriksson, P.G., 2021. Bipedal leaping Jurassic vertebrates in Southern Africa: proposed new ichnotaxon and inferred palaeoenvironment:. Trans. R. Soc. South Africa 76 (3), 235–245.
Veldmeijer, A.J., 2003a. Description of *Coloborhynchus spielbergi* sp. nov. (Pterodactyloidea) from the Albian (Lower Cretaceous) of Brazil. Scr. Geol. 125 (35), e139.
Veldmeijer, A.J., 2003b. Preliminary description of a skull and wing of a Brazilian Cretaceous (Santana Formation; Aptian-Albian) pterosaur (Pterodactyloidea) in the collection of the AMNH: PalArch's. Journal of Vertebrate Palaeontology, 1–14.
Veldmeijer, A. J., Signore, M., and Meijer, H., 2005a, *Brasileodactylus* (Pterosauria, Pterodactyloidea, Anhangueridae); an update: Cranium, v. 22, no. 1, p. 45-56.
Veldmeijer, A. J., Signore, M., and Meijer, H. J., 2005b, Description of two pterosaur (Pterodactyloidea) mandibles from the lower Cretaceous Santana Formation, Brazil: Deinsea, v. 11, no. 1, p. 67-86.
Veldmeijer, A.J., Meijer, H., Signore, M., 2006. *Coloborhynchus* from the Lower Cretaceous Santana Formation, Brazil (Pterosauria, Pterodactyloidea, Anhangueridae); an update: PalArch's. Journal of Vertebrate Palaeontology 3 (2), 15–29.
Veldmeijer, A.J., Meijer, H.J., Signore, M., 2009. Description of Pterosaurian (Pterodactyloidea: Anhangueridae, *Brasileodactylus*) remains from the Lower Cretaceous of Brazil. Deinsea 13 (1), 9–40.
Vila Nova, B.C., Sayão, J.M., Neumann, V.H.M.L., Kellner, A.W.A., 2014. Redescription of *Cearadactylus atrox* (Pterosauria, Pterodactyloidea) from the Early Cretaceous Romualdo Formation (Santana Group) of the Araripe Basin, Brazil. J. Vertebr. Paleontol. 34 (1), 126–134.
Vila Nova, B., Sayão, J., Langer, M., Kellner, A., 2015. Comments on the cervical vertebrae of the Tapejaridae (Pterosauria, Pterodactyloidea) with description of new specimens:. Hist. Biol. 27 (6), 771–781.
Vullo, R., Marugán-Lobón, J., Kellner, A. W., Buscalioni, A. D., Gomez, B., De La Fuente, M., and Moratalla, J. J., 2012, A new crested pterosaur from the Early Cretaceous of Spain: the first European tapejarid (Pterodactyloidea: Azhdarchoidea): PLoS One, v. 7, no. 7, p. e38900.
Wagstaff, B., McEwen Mason, J., 1989. Palynological dating of Lower Cretaceous coastal vertebrate localities, Victoria, Australia:. Nat. Geog. Res. 5 (1), 54–63.
Wang, X., Zhou, Z., 2003b. A new pterosaur (Pterodactyloidea, Tapejaridae) from the Early Cretaceous Jiufotang Formation of western Liaoning, China and its implications for biostratigraphy: Chin. Sci. Bull. 48 (1), 16–23.
Wang, X., Kellner, A.W., Zhou, Z., de Almeida Campos, D., 2005. Pterosaur diversity and faunal turnover in Cretaceous terrestrial ecosystems in China. Nature 437 (7060), 875–879.
Wang, X., Campos, D.D.A., Zhou, Z., Kellner, A.W., 2008. A primitive istiodactylid pterosaur (Pterodactyloidea) from the Jiufotang Formation (Early Cretaceous), northeast China. Zootaxa 1813, 1–18.
Wang, X., Kellner, A.W., Jiang, S., Meng, X., 2009. An unusual long-tailed pterosaur with elongated neck from western Liaoning of China. An. Acad. Bras. Cienc. 81 (4), 793–812.
Wang, X., Kellner, A.W., Jiang, S., Cheng, X., Meng, X., Rodrigues, T., 2010. New long-tailed pterosaurs (Wukongopteridae) from western Liaoning, China. An. Acad. Bras. Cienc. 82 (4), 1045–1062.
Wang, X., Jiang, S., Zhang, J., Cheng, X., Yu, X., Li, Y., Wei, G., Wang, X., 2017. New evidence from China for the nature of the pterosaur evolutionary transition. Sci. Rep. 7 (1), 42763.
Wang, X.L., Zhou, Z.H., 2003a. Two new pterodactyloid pterosaurs from the Early Cretaceous Jiufotang Formation of western Liaoning. China: Vertebrata PalAsiatica 41 (1), 34–49.
Wellnhofer, P., 1970. Die Pterodactyloidea (Pterosauria) der Oberjura-Plattenkalke Suddentschlands, Bayer. Akad. Wiss. Math. Nat. Klasse Nf. H, v, Bayer, p. 141.
Wellnhofer, P., 1985. Neue Pterosaurier aus der Santana-Formation der Chapada do Araripe, Brasilien:. Palaeontographica Abteilungen A 187, 105–182.
Wellnhofer, P., 1988. Terrestrial locomotion in pterosaurs. Hist. Biol. 1 (1), 3–16.
Wellnhofer, P., 1991. Weitere Pterosaurierfunde aus der Santana-Formation (Apt) der Chapada do Araripe, Brasilien: Palaeontographica. Abteilung A, Paläozoologie, Stratigraphie 215, 43–101.
Wellnhofer, P., 1991b. The illustrated encyclopedia of pterosaurs. Crescent Books.
Wellnhofer, P., 1991c. The Santana Formation Pterosaurs: MaiseyJ Ged. Santana Fossils: An Illustrated Atlas. TFH Publications, NewJersey, pp. 351–371.
Wellnhofer, P., Buffetaut, E., 1999. Pterosaur remains from the Cretaceous of Morocco. Paläontol. Z. 73 (1–2), 133–142.
Wellnhofer, P., Kellner, A., 1991. The skull of *Tapejara wellnhoferi* Kellner (Reptilia, Pterosauria) from the Lower Cretaceous Santana Formation of the Araripe Basin, Northeastern Brazil. : Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 31, 89–106.
Wellnhofer, P., 1977. *Araripedactylus dehmi* nov. gen., nov. sp., ein neuer Flugsaurier aus der Unterkreide von Brasilien:. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 17, 157–167.
Wellnhofer, P., 1978, Pterosauria, Lubrecht & Cramer Ltd.
Wellnhofer, P., 1987. New crested pterosaurs from the Lower Cretaceous of Brazil:. Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie 27, 175–186.
Wellnhofer, P., 2008, A short history of pterosaur research: Zitteliana, p. 7-19.
Wiffen, J., and Molnar, R., 1988, First pterosaur from New Zealand: Alcheringa, v. 12, no. 1, p. 53-59.
Williams, C. J., Pani, M., Bucchi, A., Smith, R. E., Kao, A., Keeble, W., Ibrahim, N., and Martill, D. M., 2021, Helically arranged cross struts in azhdarchid pterosaur cervical vertebrae and their biomechanical implications: iScience, v. 24, no. 4, p. 102338.
Witton, M.P., 2008. A new azhdarchoid pterosaur from the Crato Formation (Lower Cretaceous, Aptian?) of Brazil. Palaeontology 51 (6), 1289–1300.
Witton, M.P., 2013. Pterosaurs: natural history, evolution, anatomy. Princeton University Press.
Witton, M.P., 2009. A new species of *Tupuxuara* (Thalassodromidae, Azhdarchoidea) from the Lower Cretaceous Santana Formation of Brazil, with a note on the nomenclature of Thalassodromidae. Cretac. Res. 30 (5), 1293–1300.
Wu, W.H., Zhou, C.F., Andres, B., 2017. The toothless pterosaur *Jidapterus edentus* (Pterodactyloidea: Azhdarchoidea) from the Early Cretaceous Jehol Biota and its paleoecological implications. PLoS One 12 (9), e0185486.
Yates, A.M., Hancox, P.J., Rubidge, B.S., 2004. First record of a sauropod dinosaur from the upper Elliot Formation (Early Jurassic) of South Africa:. S. Afr. J. Sci. 100 (9), 504–506.
Yates, A.M., Bonnan, M.F., Neveling, J., Chinsamy, A., Blackbeard, M.G., 2010. A new transitional sauropodomorph dinosaur from the Early Jurassic of South Africa and the evolution of sauropod feeding and quadrupedalism:. Proc. R. Soc. B: Biol. Sci. 277 (1682), 787–794.

Zanettini, J.C.M., Leanza, H.A., Giusiano, A., Santamaría, G.R., Franchi, M., 2010. Hoja Geológica 3972-II, Loncopué, provincia del Neuquén. Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino Boletín 381, 93.
Zhang, X., Jiang, S., Cheng, X., Wang, X., 2019. New Material of *Sinopterus* (Pterosauria, Tapejaridae) from the Early Cretaceous Jehol Biota of China. Anais da Academia Brasileira de Ciências v., 91

Adele H. Pentland is a palaeontologist at the Australian Age of Dinosaurs Museum of Natural History (AAOD) in Winton, central western Queensland and part-time PhD student at Swinburne University of Technology. Her Ph. D. on pterosaurs from the early to mid-Cretaceous of eastern Australia has resulted in the description of *Ferrodraco lentoni*, the most complete Australian pterosaur to date. Outside of her Ph.D. Adele has also worked on sauropod and theropod dinosaurs, as well as exceptionally preserved insects in amber.

Stephen F. Poropat (Ph.D., Monash University, Australia) is a palaeontologist based in the School of Earth and Planetary Sciences at Curtin University, Western Australia. Although his Ph.D. focused on Cretaceous ostracods from Brazilian offshore basins, his subsequent postdoctoral research has largely centred around mid-Cretaceous reptiles, particularly from eastern Australia. Much of this work has focused on sauropod dinosaurs, but Stephen has also worked on theropod and ornithopod dinosaurs, as well as crocodyliforms, pterosaurs, and turtles. Stephen is now working on exceptional fossil preservation with Professor Kliti Grice and her team at the Western Australian Organic and Isotope Geochemistry Centre (Curtin University).